aspects of establishment and retention, and proximate mechanisms. Behaviour 85:157–183.
FORESTER, D. C., AND A. WISNIESKI. 1991. The significance of airborne olfactory cues to the recognition of home area by the dart-poison frog, *Dendrobates pumilio*. J. Herpetol. 25:502–504.
LIMERICK, S. 1980. Courtship behavior and oviposition of the poison-arrow frog *Dendrobates pumilio*. Herpetologica 36:69–71.
MCVEY, M. E., R. C. ZAHARY, D. PERRY, AND J. MACDOUGAL. 1981. Territoriality and homing behavior in the poison dart frog (*Dendrobates pumilio*). Copeia 1981:1–8.
SAVAGE, J. M. 1968. The dendrobatid frogs of Central America. Copeia 1968:745–776.
NUNES, V. D. A., AND R. G. JAEGER. 1989. Salamander aggressiveness increases with length of territorial ownership. Copeia 1989:712–718.
WEYGOLDT, P. 1980. Complex brood care and reproductive behavior in captive poison-arrow frogs, *Dendrobates pumilio* O. Schmidt. Behav. Ecol. Sociobiol. 7:329–332.
ZAR, J. H. 1974. Biostatistical Analysis. Prentice Hall, Englewood Cliffs, New Jersey.

Accepted: 9 April 1992
Associate Editor: H. Carl Gerhardt

Herpetologica, 49(1), 1993, 99–107

CANNIBALISM IN THE AMERICAN ALLIGATOR

WILLIAM L. ROOTES AND ROBERT H. CHABRECK

School of Forestry, Wildlife, and Fisheries,
Louisiana State University Agricultural Center,
Baton Rouge, LA 70803, USA

ABSTRACT: Cannibalism in the American alligator (*Alligator mississippiensis*) was evaluated in Louisiana by examining 706 alligator stomachs for web tags previously attached to smaller alligators. Alligators >2.73 m total length (TL) were more cannibalistic than smaller alligators. Large alligators (>2.73 m) preyed almost exclusively on large juveniles and small adults (1.22–2.12 m TL). Medium-sized alligators (2.13–2.73 m TL) preyed principally on medium-sized juvenile alligators (0.75–1.20 m TL), while small alligators (1.35–2.12 m TL) preyed mainly on hatchlings and small juveniles (<0.75 m TL). Alligators <1.35 m TL were not cannibalistic. We consider cannibalism an important population regulating mechanism and estimated that cannibalism accounted for 50.2% of total hatchling mortality and 63.7% of total mortality in alligators of age 11 mo and older. Mortality due to cannibalism appeared to be distributed proportionately among all cohorts in the 0.35–2.12 m TL size classes, resulting in a relatively uniform reduction across the group; males and females were cannibalized in the same proportions as they occurred in the population. Cannibalism accounted for only a small part of each predator's diet. Total losses due to cannibalism were an estimated 2.13 prey alligators per potential predator in the standing crop per year.

Key words: American alligator; *Alligator mississippiensis*; Cannibalism; Population regulation; Mortality; Behavior

INTRASPECIFIC predation, the process of killing and eating an individual of the same species, was once considered aberrant behavior (Fox, 1975). A growing body of evidence now indicates that cannibalism is not only common, but is an important behavior of many species. Polis (1981) reported that cannibalism occurred in over 1000 species. It has been shown to influence strongly the competitive interactions, dynamics, and life histories of some populations (Polis and Myers, 1985).

Cannibalism in the American alligator has been reported by several authors (Delany and Abercrombie, 1986; Giles and Childs, 1949; Nichols et al., 1976; Taylor, 1986; Valentine et al., 1972). These reports were associated with studies of food habits, and no effort has been made to determine the extent of the behavior or its impact on the population dynamics of the species. The purpose of our study was to determine the extent of cannibalism in a marsh-population of alligators believed to be at or near carrying capacity and to evaluate the possible role of cannibalism in influencing demographic structure and population processes.

Methods and Materials

Study Area

The study was conducted on Lacassine National Wildlife Refuge in southwestern Louisiana. A 6478-ha, permanently flooded impoundment located within the refuge served as the principal study site. The impoundment, referred to as Lacassine Pool, consisted of fresh marsh interspersed with shallow ponds, ditches, and canals. Dense, emergent stands of maidencane (*Panicum hemitomon*), bulltongue (*Sagittaria lancifolia*), and spikerush (*Eleocharis* spp.) dominated the marsh. Open areas of water ranged from 0.3–1.0 m deep and contained submerged and floating plants. Precipitation constituted the only source of water to the pool. Excess water was allowed to escape over three spillways located along the impoundment's perimeter levees.

From the inception of the Refuge in 1937 through 1982, hunting of alligators was prohibited. An annual selective commercial harvest was initiated in 1983. Between 1983 and 1986, 481 alligators >1.21 m total length (TL) were harvested.

Collection of Data

We determined cannibalism by recovering web tags of marked alligators from the stomachs of other alligators. Each year from 1981 through 1988, approximately 600 alligators ranging in size from 0.35–3.20 m TL were captured, tagged, and released in Lacassine Pool. We captured alligators by methods described by Chabreck (1963) and determined sex by cloacal examination for most alligators >0.45 m TL (Chabreck, 1963). Total length was measured along the alligator's dorsal surface. Each alligator was marked with three like-numbered monel web tags. Web tags were approximately 10 mm long and 2 mm wide. One tag was attached to the webbing of each hind foot, and one was attached to the webbing of a front foot.

Alligator eggs hatch in August in Lacassine Pool (Carbonneau, 1987), and because tagging was usually conducted during July and August each year, the youngest marked alligators were approaching 1 yr of age. On 1 September 1987, 131 hatchlings were captured, tagged, and released at eight nest sites.

We collected stomachs from alligators captured during a commercial harvest held in the pool in September 1987 and 1988. In 1987, we collected 255 stomachs; 451 were collected in 1988. Alligators were captured by contract trappers using baited hooks. Legal restrictions limited the harvest, and thus the sample, to alligators ≥1.21 m TL. We determined the total length, mass, and sex of each harvested alligator. After each alligator was skinned, its stomach was removed and frozen for later analysis. Stomachs were radiographed with standard X-ray equipment, and stomachs that contained web tags were opened and the tags were recovered.

We determined the percentage of tagged alligators in the population from recapture rates during the 1987 and 1988 harvest and summer tagging programs. Because most alligators captured during the 1987 and 1988 tagging programs were <1.21 m TL and all harvested alligators were >1.21 m TL, we calculated two recovery rates for each year. An overall rate was estimated by adjusting for each group's representative share of the total population.

Calculations of cannibalism mortality rates were based on the assumption that tags found in alligator stomachs represented cannibalism of tagged alligators that occurred during the 12 mo prior to the harvest of the predatory alligator. To test this assumption and determine how rapidly web tags actually passed through the stomachs of predatory alligators, baits with tags but no hooks were fed to alligators. Baits were suspended 0.30 m above the water. A numbered steel washer, 4 cm in diameter and considered too large to pass through an alligator's stomach, and two

numbered monel web tags were attached to each bait. Alligators took 100 baits between 3 August and 9 August 1988. We recovered washers and bait tags from stomachs by the same method used to recover web tags.

Size-class distribution of the alligator population in Lacassine Pool was determined by night counts (Chabreck, 1966). Five randomly selected transects were traveled by airboat across the pool between 30 July and 12 August 1988. Alligators were spotted using a 28,000 lux Q-beam light. All alligators visible from the transect line were counted. Total length of each alligator was estimated by methods described by Chabreck (1966).

The 1988 pre-hatching alligator population was estimated from nest counts (Chabreck, 1966). On 10 July 1988, 12 transects were flown across Lacassine Pool in a fixed wing aircraft so that 25% of the pool was surveyed. We counted alligator nests within 100 m of each side of the plane from an altitude of 61 m at an air speed of 130 km/h. We divided the number of nests counted by the percentage of the pool within the transect boundaries to determine total nests.

The total alligator population of Lacassine Pool was computed with the following formula presented by Chabreck (1966):

$$P = \frac{N}{AFE}$$

where, P = total alligator population, N = total number of alligator nests, A = percentage adults in population, F = percentage of adults that are females, and E = percentage of adult females that nested.

Percentage of adults (alligators >1.82 m TL) in the population (A) was determined from size-class data collected during night counts. Percentage of adults that were females (F) was determined from 1009 adult alligators captured during the 1983 through 1988 harvest program in the pool. Percentage of adult females that nested (E) was determined from 15 radio-collared adult females monitored in the pool during summer 1988 (Rootes, 1989). A life table (Downing, 1980) was used to calculate total mortality of alligators age 11 mo and older. The life table was derived from the size-class distribution determined by night counts and age and length data for alligators in Lacassine Pool presented by Rootes et al. (1991).

Statistical Analysis

Chi-square (Steel and Torrie, 1980) was used to test for differences in the percentage of marked alligators in the population between years, cannibalism between sexes and among size classes of alligators, and web tag retention rates between sexes and among size classes. We used PROC GLM (SAS Institute Inc., 1985) to regress the TL of prey alligators on the TL of their predators. We used a binomial probability function (Hogg and Tannis, 1977) to estimate the probability that a web tag would be retained in a predatory alligator stomach after 6 mo and 1 yr. Prey alligators were assumed to have been cannibalized 6 mo prior to the predator's harvest or on the date that they were tagged, whichever occurred last. Growth of alligators marked more than 6 mo before the predator's harvest was projected by growth curves presented by Rootes (1989).

Results

Of 1031 alligators captured during the 1987 summer tagging program and fall harvest season, 129 were previously tagged. Of 1077 captured in 1988, 139 were tagged. Based on these recoveries, tagged alligators comprised 14.2% of the total alligator population in 1987 and 14.4% of the population in 1988 and did not differ between years ($\chi^2 = 0.075$, df = 1, $P = 0.79$). No difference was found between years ($\chi^2 = 1.60$, df = 1, $P = 0.21$) in cannibalism rates of alligators of marked age 11 mo and older (Table 1); therefore, data were pooled across years to compare sexes and size classes of predators. No difference was found between the number of cases of cannibalism by 1.22–2.73 m TL males and females of the same size ($\chi^2 = 0.27$, df = 27, $P = 0.62$); therefore, data were pooled across sex. A comparison of the pooled group to alligators >2.73 m TL disclosed that larger alligators (males) were more

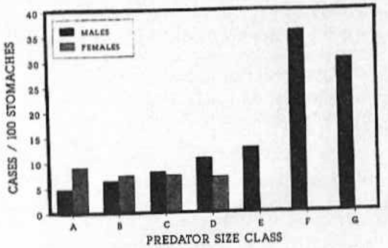

FIG. 1.—Index of cannibalism by size class and sex of predatory alligator, Lacassine Pool, 1987 and 1988. Predator size class (m TL): A = 1.22–1.51, B = 1.52–1.82, C = 1.83–2.12, D = 2.13–2.42, E = 2.43–2.73, F = 2.74–3.04, G = >3.04.

cannibalistic (χ^2 = 56.38, df = 1, $P <$ 0.0001) (Fig. 1). Alligators >2.73 m TL contributed 13.6% of the stomachs examined but accounted for 41.0% of the cases of cannibalism identified. No females >2.73 m TL were found on the study area.

Retention Rate of Web Tags

Calculations of cannibalism mortality were based on the assumption that web tags found in stomachs represented cannibalism of tagged alligators during the 12 mo prior to the predator's harvest. Data from baited washers tended to support this assumption. Washers from 46 of the 100 baits taken in August 1988 were recovered from stomachs of alligators harvested in September 1988. No difference was found in the rate at which web tags were lost from stomachs of different size classes of alligators (χ^2 = 1.63, df = 4, P = 0.81) or males and females (χ^2 = 0.66, df = 1, P = 0.77). Harvested males and females each ingested 46 web tags, males passed 10 web tags and females passed nine web tags. Passage of a single tag was found to be independent of the number of tags present (χ^2 = 0.87, df = 2, P = 0.33).

Of 92 web tags ingested, 20.7% were eliminated in 39.7 ± 3.6 (SD) days. In all cases, at least one of the two web tags ingested was retained; therefore, predation of a tagged alligator would have been identified. If the probability of eliminating a web tag is assumed to be a constant 0.21 during each successive 40-day period, the probability that one web tag would be retained in an alligator's stomach after 6 mo would be 0.35, and the probability of retaining one web tag for 1 yr would be 0.12.

Chabreck and Joanen (1979) noted that alligators in southern Louisiana do not feed during winter dormancy, approximately November through February, and feed only occasionally during October and March. Therefore, 6 mo would elapse between the resumption of normal feeding activity and the end of the fall harvest. With an expected 35% retention rate after 6 mo, the probability of a harvested alligator retaining at least one of the three web tags from a marked alligator eaten immediately after the resumption of normal feeding activity would be 0.725. Conversely, the probability of retaining at least one of three web tags ingested during the 2 mo before the end of normal feeding the previous fall would be 0.31. The probability of retaining at least one web tag for more than 1 yr would be 0.32.

TABLE 1.—Cannibalism of marked alligators that were age 11 mo and older and identified from stomach contents of alligators taken from Lacassine Pool, 1987 and 1988.

	1987		1988		Combined years	
Predator total length (m)	No. stomachs examined	Cases of cannibalism identified	No. stomachs examined	Cases of cannibalism identified	No. stomachs examined	Cases of cannibalism identified
1.22–1.51	29	2	46	2	75	4
1.52–1.82	53	1	92	9	145	10
1.83–2.12	63	3	127	12	190	15
2.13–2.42	53	4	92	7	145	11
2.43–2.73	24	1	31	5	55	6
2.74–3.04	15	5	35	13	50	18
>3.04	18	7	28	7	46	14
Total	255	23	451	55	706	78

These calculations suggest that we missed some cases of cannibalism of tagged alligators that occurred during the 12 mo prior to harvest. However, it appears that a similar number of cases of cannibalism that occurred during preceding years were included. We assumed that web tags found in stomachs approximated actual cannibalism rates during the preceding year.

Alligator Population Estimate

A total of 67 alligator nests was counted during the 1988 nest survey of Lacassine Pool. Approximately 25% of the area was sampled; consequently, the total number of nests in the pool (N) was estimated to be 268.

Of the 931 alligators sighted during 1988 night counts, 15.5% were of adult size (A). Of the 1009 adult alligators harvested from the pool between 1983 and 1988, 38.9% were females (F). Rootes (1989) estimated that 29.9% of the adult females in Lacassine Pool nested (E) in 1988. Although the number of adult females examined in Lacassine Pool was small (19), estimates of the proportion of adult females nesting compares favorably with studies elsewhere. Taylor et al. (1991) examined 780 adult-sized female alligators on Marsh Island, Louisiana, and found that 25.3% had nested. Wilkinson (1985) reported that 27.5% of 69 adult females in South Carolina nested. Dividing total nests (N) by AFE (0.155 × 0.389 × 0.299) yielded a July 1988 population estimate of 14,866 alligators.

Cannibalism Mortality in Hatchling Alligators

Web tags from five of the 131 hatchling alligators marked in September 1987 were recovered from stomachs of alligators harvested in September 1988. Of the estimated 5036 harvestable-size alligators in the pool (Table 2), we examined stomachs from 451 (Table 1). Dividing five by the proportion of total predatory alligators sampled (0.09) indicated that 55 marked hatchlings were cannibalized. If unmarked hatchlings were cannibalized at the same rate as marked hatchlings, 42.0% of all hatchlings would be lost to cannibalism during the first year of life. Carbonneau (1987) estimated that total hatchling mortality in Lacassine Pool was 83.6% by age 1 yr. Based on this estimate, 50.2% of total hatchling mortality would be attributed to cannibalism.

TABLE 2.—Estimate of July 1988 alligator population, Lacassine Pool, 1988.

Total length of alligator (m)	% total alligators sighted during night counts*	July 1988 alligator population
<0.92	48.2	7165
0.92–1.21	18.0	2676
1.22–1.51	9.8	1457
1.52–1.82	8.5	1264
1.83–2.12	6.0	892
2.13–2.42	5.6	832
2.43–2.73	1.9	282
2.74–3.04	1.1	164
>3.04	0.9	134
Total	100.0	14,866**

* A total of 931 alligators were counted during 1988 night counts.
** As determined from nest counts.

Cannibalism Mortality in Older Alligators

A total of 3288 alligators 11 mo and older were cannibalized from September 1987 through August 1988 (Table 3). Assuming constant recruitment and age specific mortality rates, cannibalism mortality was 22.1% of the standing crop. Total mortality was 5164 or 34.7% (5164/14,866) of the standing crop (Table 4). Based on this estimate, cannibalism accounted for 63.7% of total mortality of alligators age 11 months and older. Although cannibalism accounted for a substantial portion of total mortality, prey alligators comprised a minor portion of each predator's diet. An estimated 5025 potential predators (alligators >1.21 m TL, Table 2) were in the July 1988 population, and each consumed an average of 0.65 alligator per year.

Carbonneau (1987) estimated that 23.8 alligators hatched per nest in Lacassine Pool in 1986. Applying this rate to 704 nests present in 1987 (Carbonneau, 1987), 16,755 hatchlings would have been available to predators in September 1987. With a 42.0% cannibalism mortality rate, an estimated 7037 hatchlings were cannibalized by

TABLE 3.—Size class (m TL) distribution of cannibalistic alligators, Lacassine Pool, 1988.

(A) TL of cannibalistic alligator (m)	(B) Cases of cannibalism identified[a]	(C) % size class sampled[b]	(D) % population marked[c]	(E) Total cases of cannibalism[d]	(F) % total cannibalism cases
1.22–1.51	2	3.2	14.4	434	13.2
1.52–1.82	9	7.3	14.4	856	26.1
1.83–2.12	12	14.2	14.4	586	17.8
2.13–2.42	7	11.0	14.4	442	13.4
2.43–2.73	5	11.0	14.4	316	9.6
2.74–3.04	13	21.3	14.4	423	12.9
>3.04	7	21.0	14.4	231	7.0
Total	55	N/A	N/A	3288	100.0

[a] From stomach content analysis (Table 1).

[b] $\frac{\text{Number of stomachs analyzed in size class (Table 1)}}{\text{Pre-harvest population in size class (Table 2)}}$

[c] As determined from recapture rates during 1988 tagging and harvest program.

[d] $\frac{\text{Column B}}{\text{Column C} \times \text{Column D}}$

predators during the year ended 31 August 1988 or 1.40 hatchlings per predator in the standing crop per year. Total cannibalism of all size classes of alligators was 2.05 prey per predatory alligator in the standing crop per year.

Predator Size versus Prey Size

Regression of length of prey alligators on length of predatory alligators (Fig. 2) indicates a significant linear relationship between the two groups ($F = 108.7$, df = 1, 70, $P < 0.0001$). Slope differed from zero ($P < 0.0001$), and 60.8% of the variation in the length of prey alligators (R^2) was accounted for by the length of predators. Only three of the 30 prey alligators cannibalized by predators >2.73 m TL were <1.0 m TL and may have been consumed earlier by predatory alligators that subsequently became prey themselves. If these outlying points are dropped from analysis, R^2 increases to 0.704.

Marked hatchlings ($n = 5$) were cannibalized by alligators <1.78 m TL. Mean prey size was 0.53 ± 0.18 m ($n = 28$) for predators 1.22–2.12 m TL, 1.06 ± 0.40 m ($n = 13$) for predators 2.13–2.73 m TL, and 1.49 ± 0.42 m ($n = 31$) for predators >2.73 m TL.

The mean TL of alligators at hatching is 0.23 m (Chabreck and Joanen, 1979), and the predicted minimum predator size was 1.35 m TL (Fig. 1). However, no web tags were recovered from stomachs of alligators <1.40 m TL, which was slightly larger than the minimum legal size (1.21 m TL). Based on the regression model, alligators may be victims of cannibalism until they reach a TL of approximately

TABLE 4.—Total annual mortality of alligators age 11 mo and older, Lacassine Pool.

Size class (m)	Total number in size class*	$\bar{x}$ age of individuals in size class (mo)**	Reduction from previous size class	Time elapsed (mo)	Annualized mortality
<0.92	7165	18	N/A	N/A	N/A
0.92–1.21	2676	34	4489	16	3367
1.22–1.51	1457	47	1219	13	1125
1.52–1.82	1264	62	193	15	154
1.83–2.12	892	81	372	19	234
2.13–2.42	832	101	60	20	35
2.43–2.73	282	134	550	33	200
2.74–3.04	164	169	118	35	40
>3.04	134	209	30	41	9
Total	14,866	N/A	N/A	N/A	5164

* From Table 2.

** Taken from age specific length curves derived by Rootes (1989) from 1981–1988 mark-recapture data collected on alligators in Lacassine Pool.

2.13 m, assuming a maximum predator size of 4.0 m (Rootes, 1989). Web tags from four alligators approaching 2.13 m long were recovered from stomachs. All three web tags from a 2.08-m male that was tagged in May 1988 were recovered from the stomach of a 2.85-m male harvested in September 1988. Although the TL of the predator was only slightly greater (37%) than the TL of the prey, the mass was substantially greater (208%).

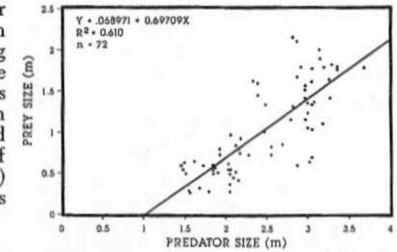

FIG. 2.—Relationship between total length of predatory alligators and total length of prey alligators, Lacassine Pool, 1987 and 1988.

Sex Ratio of Prey

The sex ratio of prey alligators did not differ from the sex ratio of the general population ($\chi^2 = 0.431$, df = 1, $P = 0.52$). Of 4610 alligators captured during the tagging program, 63% were males. Sex was known for 43 of the prey alligators; 60.1% were males. Prey cannibalized by male alligators were 61.1% males ($n = 36$), and prey of female alligators were 57.1% males ($n = 7$).

DISCUSSION

Cannibalism accounted for >50% of total mortality among alligators in Lacassine Pool and appeared to be a major population regulating mechanism. The relationship of cannibalism to alligator populations in other areas would depend on several factors. Cannibalistic behavior is generally considered to be density related. For some species, rates of cannibalism are consistent with simple encounter models in which the probability of attack is proportioned to the probability of encountering a vulnerable individual (Fox, 1975). A common effect of high density is food shortage, which also may increase cannibalistic behavior. Decreasing food availability would likely increase foraging activity, lower attack thresholds, expand diets beyond normal limits, and leave alligators deprived of food weakened and increasingly vulnerable to cannibalism (Polis, 1981). Low growth rates (Rootes, 1989), poor mass-length ratios (Rootes, 1989), and high densities relative to other alligator populations in Louisiana (Chabreck, 1985) occurred in Lacassine Pool. Nevertheless, we believe that most cannibalized alligators were taken alive and not scavenged after dying of other causes.

Many areas within the range of the American alligator have an alligator density similar to that of Lacassine Pool (Chabreck, 1985). We believe that cannibalism is a major factor regulating alligator densities in those areas as well as in Lacassine Pool. In fact, cannibalism was noted in studies of food habits from areas with a density considerably less than that of Lacassine Pool (McNease and Joanen, 1977; Taylor, 1986). Nichols et al. (1976) stated that cannibalism was a major density dependent factor acting on alligators in Louisiana, and they estimated that annual mortality rates from cannibalism ranged from 2–6%. Delany and Abercrombie (1986) recovered 20 web tags in Florida from stomachs of 350 alligators (mean TL = 2.4 m) but did not indicate the number of tagged alligators in their study area.

Large alligators (>2.73 m TL) were 4.4 times (Table 1) more cannibalistic than smaller, harvestable-sized alligators. Large alligators made up only 2.0% (Table 2) of the total population but accounted for 41.0% (Table 1) of the total cannibalism cases. Large alligators preyed principally on large juveniles and small adult alligators (1.21–2.12 m TL), but avoided hatchlings completely, and took very few alligators <1.21 m TL.

Several factors could account for the absence of hatchlings through medium-sized juveniles (0.24–1.21 m TL) in the diets of large alligators. The energy gained by cannibalizing a small juvenile may not be worth the energy expended to capture it.

Habitat partitioning by different-sized alligators could reduce the chance of encounters between large alligators and small juveniles. Cott (1961) reported that Nile crocodiles from 2–5 yr old avoided cannibalism by retreating to habitat not frequented by larger crocodiles.

Unlike most reptiles, the female American alligator aggressively guards her hatchlings (McIlhenny, 1935). This behavior may have developed because of predation on hatchlings by other alligators. Juvenile alligators often remain at the den of their mother after a second brood hatches the following year (Chabreck, 1965). At that age (1 yr), they do not prey on hatchlings. By the time that juveniles are large enough to prey on hatchlings, most have left the mother's den (Chabreck, 1965; Rootes, 1989). They are perhaps driven away by the mother as part of her behavior of guarding hatchlings. In spite of maternal protection, many hatchlings were cannibalized in Lacassine Pool.

The size relationship between predatory and prey alligators, the relative abundance of each size class in the population, and the estimate that males and females were cannibalized in the same proportion as they occurred in the population have important implications for regulation of the population size structure. Large adults accounted for 19.9% of total cannibalism cases and preyed on cohorts that represent 23% (Table 3) of the standing crop. Medium-sized predators (2.13–2.73 m TL) accounted for 23% of the cannibalism cases and preyed principally on medium-sized juveniles (0.75–1.21 m TL) that comprised 25% of the standing crop. Small predators (1.22–2.12 m TL) accounted for 57% of the total cases of cannibalism and preyed on small juveniles (0.35–0.74 m TL) that comprised 46% of the standing crop. This suggests that cannibalism mortality results in a relatively uniform reduction among all cohorts in the 0.35–2.12 m TL group without causing any one cohort to be eliminated or become dominant. Cannibalism mortality could have a stabilizing effect on future populations by insuring reduced but relatively uniform recruitment into the adult group (>2.12 m TL).

Larger home ranges (Joanen and McNease, 1972) and a more aggressive nature (Guggisberg, 1972) suggest that large adult males dominate male breeding. Clutch size and the probability of nesting increase as the size of adult female alligators increase (Wilkinson, 1985). Through reduced competition and increased nutrition, cannibalistic behavior in alligators would enhance individual fitness by improving survival of the most reproductively active adults (>2.12 m TL) while insuring a reduced but relatively uniform recruitment into this group over time.

Cannibalism that is distributed over a range of size classes instead of being concentrated on the very smallest individuals may improve population energetics. Polis (1981) pointed out that when food is limiting to adults, cannibalism can serve as an energy loop, which maintains calories in a population, particularly when immature alligators feed on resources that are inaccessible to or underutilized by adults. Small juvenile alligators prey principally on insects and small fishes, medium-sized juveniles feed mostly on crustaceans, and large juveniles and adults feed mainly on larger fishes, birds, and mammals (Chabreck, 1971; Delany and Abercrombie, 1986; Giles and Childs, 1949; Wolfe et al., 1987). By distributing cannibalism over a variety of prey sizes, predatory alligators in Lacassine Pool may have become more efficient in indirectly expanding their prey base.

Cannibalism among alligators in Lacassine Pool appears to be functioning as a means of limiting population size to the carrying capability of available resources. Undoubtedly food availability, density, and habitat type influence the intensity of this behavior. To fully understand the role of cannibalism in American alligator demography, populations with differing densities, nutritional conditions, and habitats should be examined.

Acknowledgments.—We thank B. W. Brown and P. Yakupzack of the U.S. Fish and Wildlife Service for supplying field equipment and other logistical support. Employees of Lacassine National Wildlife Refuge, students at Louisiana State University, and alligator hunters provided valuable assistance in collection of field data. We are grateful to Dr. V. L. Wright for his advice and assistance in the statistical analysis and interpretation of data.

Literature Cited

Carbonneau, D. A. 1987. Nesting Ecology of an American Alligator Population in a Freshwater Coastal Marsh. M.S. Thesis, Louisiana State University, Baton Rouge, Louisiana.

Chabreck, R. H. 1963. Methods of capturing, marking, and sexing alligators. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 17:47–50.

———. 1965. The movement of alligators in Louisiana. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 19:102–110.

———. 1966. Methods of determining the size and composition of alligator populations in Louisiana. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 20:105–112.

———. 1971. The foods and feeding habits of alligators from fresh and saline environments in Louisiana. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 25:117–123.

———. 1985. Cooperative Surveys of the American Alligator in the Southeastern United States during 1984. Louisiana State University, Baton Rouge, Louisiana.

Chabreck, R. H., and T. Joanen. 1979. Growth rates of American alligators in Louisiana. Herpetologica 35:51–57.

Cott, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. Trans. Zool. Soc. London 29: 211–357.

Delany, M. F., and C. L. Abercrombie. 1986. American alligator food habits in northcentral Florida. J. Wildl. Manage. 50:348–353.

Downing, R. L. 1980. Vital statistics of animal populations. Pp. 247–267. *In* S. D. Schemnitz (Ed.), Wildlife Management Techniques Manual. The Wildlife Society, Washington, D.C.

Fox, L. R. 1975. Cannibalism in natural populations. Ann. Rev. Ecol. Syst. 6:87–106.

Giles, L. W., and V. L. Childs. 1949. Alligator management on the Sabine National Wildlife Refuge. J. Wildl. Manage. 13:17–28.

Guggisberg, J. A. 1972. Crocodiles: Their Natural History, Folk Lore, and Conservation. Stackpole Books, Harrisburg, Pennsylvania.

Hogg, R. V., and E. A. Tannis. 1977. Probability and Statistical Inference. MacMillan, New York.

Joanen, T., and L. McNease. 1972. A telemetric study of adult male alligators in Rockefeller Refuge, Louisiana. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 26:252–275.

McIlhenny, E. A. 1935. The Alligator's Life History. Christopher Publishing House, Boston.

McNease, L., and T. Joanen. 1977. Alligator diets in relation to marsh salinity. Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agencies 31:36–40.

Nichols, J. D., L. Viehman, R. H. Chabreck, and B. Fenderson. 1976. Stimulation of a commercially harvested alligator population in Louisiana. Louisiana Agric. Exp. Sta. Bull. 691:1–59.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Ann. Rev. Ecol. Syst. 12: 225–251.

Polis, G. A., and C. A. Myers. 1985. A survey of intraspecific predation among reptiles and amphibians. J. Herpetol. 19:99–107.

Rootes, W. L. 1989. Behavior of American Alligators in a Louisiana Freshwater Marsh. Ph.D. Dissertation, Louisiana State University, Baton Rouge, Louisiana.

Rootes, W. L., R. H. Chabreck, V. L. Wright, B. W. Brown, and T. J. Hess. 1991. Growth rates of American alligators in estuarine and palustrine wetlands in Louisiana. Estuaries 14:489–494.

SAS Institute Inc. 1985. SAS User's Guide: Statistics. SAS Institute Inc., Cary, North Carolina.

Steel, R. E., and J. H. Torrie. 1980. Principles and Procedures of Statistics. McGraw-Hill, New York.

Taylor, D. 1986. Fall foods of adult alligators from cypress lake habitat, Louisiana. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 40:338–341.

Taylor, D., N. Kinler, and G. Linscombe. 1991. Female alligator reproduction and associated population estimates. J. Wildl. Manage. 55:682–688.

Valentine, J. M., J. R. Walther, K. M. McCartney, and L. M. Ivey. 1972. Alligator diets in the Sabine National Wildlife Refuge, Louisiana. J. Wildl. Manage. 36:809–815.

Wilkinson, P. M. 1985. Nesting ecology of the American alligator in coastal South Carolina: A study completion report. South Carolina Marine Resource Department, Charleston, South Carolina.

Wolfe, J. L., D. K. Bradshaw, and R. H. Chabreck. 1987. Alligator feeding habits: New data and a review. Northeast Gulf Sci. 9:1–8.

Accepted: 22 May 1992
Associate Editor: Daniel Formanowicz, Jr.