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Behavior of the American Alligator in a Louisiana Freshwater Marsh.

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BEHAVIOR OF THE AMERICAN ALLIGATOR IN A LOUISIANA FRESHWATER MARSH

A DISSERTATION

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by
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ABSTRACT

Stomachs from 706 alligators (Alligator mississippiensis) harvested from a southern Louisiana fresh marsh in 1987 and 1988 were examined for web tags from smaller marked alligators. Alligators < 1.35 m total length (TL) were found not to be cannibalistic. Large males (> 2.73 m TL) were significantly more cannibalistic than smaller alligators ($P < 0.0001$). Males and females were cannibalized in the same proportion they occurred in the population. Cannibalism mortality 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. Cannibalism was found to be an important population regulating mechanism, accounting for an estimated 50.2% of total hatchling mortality and 70.1% of total mortality in age 11 months and older alligators.

Male growth rates in both a palustrine marsh (Lacassine National Wildlife Refuge) and estuarine marsh (Rockefeller Refuge) marsh types were greater than female rates ($P < 0.0001$). Growth rates and weight-length ratios of alligators in estuarine marsh were greater than those of alligators in palustrine marsh ($P < 0.0001$). Age specific fecundity and survivorship rates of alligators in the palustrine marsh were less than alligators in the estuarine marsh.

The home range size and activity pattern of adult female alligators of different reproductive status were compared among seasons of the year. Home range size ($P = 0.54$) and minimum average daily movement rates ($P = 0.85$) did not differ between nesting and non-nesting

radio-collared females during the summer nesting season. No difference was found between females with and without broods in the two variables during the fall brooding season. Adult radio-collared female alligators ranged over larger areas and had greater daily average daily movement rates during the spring breeding season than during any other season of the year ($P < 0.01$). Annual home range size of the 15 adult female alligators monitored during the study was 36.2 ± 42.6 (SD) ha.

INTRODUCTION

The decline, protection, and subsequent recovery of the American alligator (Alligator mississippiensis) has generated much interest. Alligators occupy a variety of habitats including coastal marshes, fresh marshes, swamps, lakes, and rivers. Much of what is now known about alligators has been learned since 1950. Extensive research has been conducted in South Carolina, Florida, Louisiana, and Texas. Most previous studies have dealt with the species' food habits, nesting ecology, and husbandry. Information on other aspects of alligator behavior is lacking, has been collected on alligators occupying estuaries and lake habitats, or was based on limited observations. Freshwater marsh constitutes 31% of Louisiana's coastal marsh area (Chabreck 1970) and harbors 34% of the state's alligator population (McNease and Joanen 1976). At the time this study was initiated, little was known about alligator behavior, population processes, and growth in freshwater marsh systems.

This study was conducted on Lacassine Natural Wildlife Refuge in southwestern Louisiana. A permanently flooded impoundment located within the refuge served as the principle study site. The impoundment, referred to as Lacassine Pool, consists of floating fresh marsh. In 1981, an extensive alligator tagging program began at the pool. Between 1981 and 1988, over 600 alligators were captured, marked with monel web tags, measured, and sexed each year. After 4 decades of protection, a commercial alligator harvest was initiated in the pool in 1983. Lacassine Pool provided an

opportunity to study a fresh marsh alligator population that was at or near carrying capacity.

Intraspecific predation, the process of killing and eating an individual of the same species, was long considered aberrant behavior by many ecologists (Fox 1975). A growing body of evidence now indicates that cannibalism is not only common, but important in the behavior of many species. Polis (1981) noted cannibalism was normal behavior in over 1,000 species. It has been shown to strongly influence the competitive interactions, dynamics, and life histories of populations (Polis and Myers 1985).

Cannibalism in the American alligator (Alligator mississippiensis) has been reported by numerous authors (Giles and Childs 1949, Neill 1971, Valantine et al. 1972, Delany and Ambercrombie 1986, and Taylor 1986). These reports have generally been associated with alligators food habit studies. Most authors (Giles and Childs 1949, Neill 1971, Valantine 1972, and Taylor 1986) interpreted cannabilism evidence as incidental to territorial fighting or the result of alligators preying on carrion. Delany and Abercrombie (1986) performed a stomach content analysis on alligators taken from a population in Florida. Approximately 13% of the population had been marked with monel web tags as part of a mark-recapture study. The number of web tags found in the stomaches of alligators collected for the food habit study and the apparent size disparity between predator and tagged alligators, indicated that cannabilism in alligators was more than an incidental process. To

learn more about cannabilism behavior, 706 stomachs were collected from alligators harvested on Lacassine Pool in 1987 and 1988 and examined for web tags.

To compare the size of predator alligators to that of their prey, an estimate of the total length of prey alligators at or near the time they were canabilized was needed. To estimate the change in length between the time prey alligators were tagged, and the time they were cannabilized, growth curves were developed for alligators on Lacassine Pool from mark-recapture data collected on the pool between 1981 and 1988. Chabreck and Joanen (1979) reported growth information in alligators occupying estuarine habitats. The growth data collected in Lacassine Pool was compared to that collected by Chabreck and Joanen (1979).

To determine the role of cannibilistic behavior in influencing alligator demographic structure and population processes, considerable support information was needed. A formula developed by Chabreck (1986) was used to estimate the alligator population level on the pool. This information provided the basis for many of the demographic calculations made in this study. To make the necessary calculations on estimates of the percent of adult female alligators in Lacassine Pool that nest, the sex ratio of the population was needed.

Wilkerson (1985) and Taylor (1984) determined the percent of adult female alligators that nested on their study areas by tracking adult females fitted with radio transmitters. Fifteen adult females

were captured on Lacassine Pool, fitted with radio collars, and followed for this purpose. Because of the paucity of research and study of ranges and movement rates of adult female alligators in fresh marsh, this portion of the study was expanded so that seasonal comparisons of the home range and movement rates could be made among adult females in different reproductive stages.

Two sources of data were available to estimate the sex ratio of alligators in Lacassine Pool. Sex data were collected on alligators live-captured during the refuge's tagging program and alligators captured by baited hooks during the harvest program. At the time this study was initiated, no comparison of the sex ratio of alligators captured by the two methods had been made. A statistical comparison was completed as a part of this study.

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CHAPTER ONE

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RH: ALLIGATOR CANNIBALISM · Rootes

CANNIBALISM IN THE AMERICAN ALLIGATOR

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Abstract: Stomachs from 706 alligators (*Alligator mississippiensis*) harvested from a southern Louisiana fresh marsh in 1987 and 1988 were examined for web tags from smaller marked alligators. The alligators were harvested from a population at or in excess of carrying capacity and characterized by low growth rates, poor weight-length ratios, and high densities relative to other south Louisiana populations. Alligators < 1.35-m total length (TL) were found not to be cannibalistic. Large males (> 2.73 m TL) were significantly more cannibalistic than smaller alligators (P < .0001). Males and females were cannibalized in the same proportions they occurred in the population. Large alligators (> 2.73 m) preyed almost exclusively on large juveniles and small adults (1.21-2.12 m TL). Medium size predators (2.12-2.73 m TL) preyed principally on medium size juveniles (.75-1.20 m TL) while small predators (1.21-2.12 m TL) preyed mainly on hatchlings and small juveniles (> .75 m TL). Cannibalism was found to be an important population regulating mechanism, accounting for an estimated 50.2% of total hatchling

mortality and 70.1% of total mortality in age 11 months and older alligators. Cannibalism mortality 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. Cannibalism accounted for only a small part of each predator's diet. Total cannibalism losses were an estimated 2.13 prey alligators per predator size alligator in the standing crop per year.

Key Words: American alligator, *Alligator mississippiensis*, cannibalism, population regulation, mortality, behavior

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Intraspecific predation, the process of killing and eating an individual of the same species, was long considered aberrant behavior (Fox 1975). A growing body of evidence now indicates cannibalism is not only common, but important in the behavior of many species. Polis (1981) noted cannibalism was normal behavior in over 1,000 species. It has been shown to strongly influence the competitive interactions, dynamics, and life histories of populations (Polis and Myers 1985).

Cannibalism by the American alligator has been reported by several authors (Giles and Childs 1949, Neill 1971, Valentine et al. 1972, Delany and Abercrombie 1986, and Taylor 1986). These reports have been associated with food habit studies, and no effort has been made to determine the extent of this behavior or its importance in the species' biology. The purpose of this study was to determine the

extent of cannibalism in a marsh population of alligators believed to be at or in excess of carrying capacity and to evaluate the possible role of cannibalism in influencing demographic structure and population processes.

STUDY AREA

The study was conducted on the 12,869-ha Lacassine National Wildlife Refuge in Cameron Parish, southwestern Louisiana. A 6,478-ha permamently flooded impoundment located within the refuge served as the principle study site.

The impoundment, referred to as Lacassine Pool, consists of floating fresh marsh interspersed with shallow ponds and ditches. Dense, emergent stands of maidencane (Panicum hemitomon), bulltongue (Sagittaria lancifolia), and spikerush (Eleocharis spp.) dominate the marsh. Open water areas range from 0.3-1.0 m deep and contain submerged and floating plants including watershield (Brasenia schreberi), fanwort (Cabomba caroliniana), coontail (Ceratophyllum demerum), American lotus (Nelumbo lutea), and fragrant waterlily (Nymphaea odorata). Precipitation constitutes the only source of water to the pool. Excess water is allowed to escape over three spillways located along the impoundment's perimeter levees.

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

McNease and Joanen (1978) estimated that average fresh marsh habitat in southern Louisiana supported 1 alligator/5.67 ha. Lacassine Pool supported 1 alligator/0.42 ha in June 1987 (Carbonneau 1987). Growth rates (Chapter 2) and weight to length ratios (Joanen et al. 1989) of alligators in the pool were found to be significantly lower ($P < 0.01$) than in other south Louisiana marsh populations. All indications were the pool alligator population was at or in excess of carrying capacity at the time this study was initiated.

METHODS

Cannibalism was determined by recovering tags of marked alligators from the stomachs of predatory alligators. Each year from 1981 through 1988 approximately 600 alligators ranging in size from 0.35 m to 3.20 m TL were captured, tagged, and released in Lacassine Pool. The animals were captured by methods described by Chabreck (1963). Sex was determined by cloacal examination for most animals over 0.45 m (Chabreck 1963). Total length was measured along the animal's dorsal surface. Each alligator was marked with 3 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. All data were recorded prior to the animal's release.

Because tagging was usually conducted during July and August each year, the youngest marked animals were approaching one year of

age. On 1 September 1987, 131 hatchlings were captured, tagged, and released at 8 nest sites.

Stomachs were collected from alligators captured during a commercial harvest held on the pool in September 1987 and 1988. In 1987, 255 stomachs were collected; 451 were collected in 1988. Alligators were captured by contract trappers using baited hooks. Legal restrictions limited the harvest to alligators > 1.22 m TL. Stomachs from alligators < 1.21 m were not available for study. Only harvestable size (> 1.21 m TL) alligators were assumed to be cannibalistic.

Prior to removal from the area all harvested alligators were marked with a numbered harvest tag, and the total length, weight, and sex of each animal was determined (Joanen et al. 1989). All data along with the harvest tag number and date of capture were recorded. After each animal was skinned, its stomach was removed, placed in a plastic bag, identified with the harvest tag number and frozen for later analysis.

Each stomach was radiagraphed with standard X-ray equipment. Stomachs that contained tages were opened and the tags were recovered. All demographic data relative to predator and prey alligators were determined from harvest tag or web tag numbers and recorded.

The percent of web tagged animals in the population was determined from recapture rates experienced 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 animals were > 1.21 m TL, two recovery rates were calculated for each year. An overall rate was estimated by adjusting for each group's representative share of the total population.

To determine how rapidly web tags were passing through the stomachs of predator alligators, baits were suspended 0.30 meters above the water along canals in the pool, which, in previous years, had been heavily trapped. Chicken hind quarters were used as bait. A numbered steel washer, 4 cm in diameter and considered to be too large to pass through an alligator's stomach, and 2 numbered monel web tags were attached to each bait. A total of 100 baits were taken between 3 August and 9 August 1988. The washer number, tag numbers, and location of each bait were recorded along with the date the bait was taken. Stomachs collected during the September 1988 harvest were examined for washers and bait tags by the same method used to detect 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 300,000 candle Q-beam light. All animals visible from the transect line were counted. Total length of each alligator was estimated by methods described by Chabreck (1966).

The 1988 pre-harvest 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. Alligator nests within 100 m of each side of the plane were counted from an altitude of 61 m at an air speed of 130 km/hr. The number of nests counted was divided by the percentage of the pool within the transect boundaries to determine total nests.

A formula described by Chabreck (1967) was used to convert nest data to population numbers:

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

where, P = Total alligator population,

N = Total number of alligator nests,

A = Percent adults in population,

F = Percent of adults that are females, and

E = Percent of adult females that nested.

The percent of adults (alligators > 1.82 m TL) in the population was estimated from size class data collected during night counts. The percent of adults that were females was estimated from 1,009 adult alligators captured during the 1983 through 1988 harvest programs. The percent of adult females that nested was estimated from 15 radio-collared adult females monitored in the pool during summer 1988 (Rootes 1989). A life table was used to estimate total mortality of alligators age 11 months and older. The life table was derived from the size class distribution determined above, and age and length data for alligators in Lacassine Pool presented in Chapter 2.

Chi-square test of homogeneity (Steel and Torrie 1980) was used to test for differences in the percentage of marked alligators in the

population between years, cannabilism between sexes and among size classes of alligators, and web tag retention rates between sexes and among size classes. Simple linear regression was used to relate the TL of predator alligators with the TL of their cannabilized prey. A binomial probability function (Hogg and Tanis 1977) was used to estimate the possibility a web tag would be retained in predator alligator stomach after 6 months and 1 year.

RESULTS

Of 1,031 alligators captured during the 1987 summer tagging program and fall harvest season, 129 were previously tagged. Of 1,077 captured in 1988, 139 were tagged. Based on these recoveries, tagged alligators comprised 12.8% of the total alligator population in 1987 and 12.9% of the population in 1988. The percentage of marked alligators in the population did not differ between years (X^2 = 0.075, 1 df, P = 0.79). No difference in cannibalism of marked age 11 months and older alligators was found between years (X^2 = 1.60, 1 df, P = 0.21) (Table 1). Years were pooled to make comparisons between sexes and among size classes of predators.

Tags from 78 marked alligators were found in the 706 stomachs that were radiographed. The remains of 3 untagged alligators were found in 97 stomachs that were opened and examined in detail. Untagged alligators were not included in this analysis. No difference was found between the number of cases of cannibalism identified in 1.21-2.73 m TL males and in females of the same size (X^2 = 0.27, 1

df, P = 0.62). These two groups were pooled, and a comparison of the pooled group to males longer than 2.73 m TL disclosed that larger males were more cannibalistic (X^2 = 56.38, 1 df, $P < 0.0001$) (Figure 2).

Retention Rate of Web Tags

Washers from 46 of the 100 baits taken in August 1988 were recovered from the stomachs of alligators harvested in September 1988 (Table 2). No difference was found in the rate at which tags pass through the stomachs of different size classes of alligators (X^2 = 1.63, 4 df, P = 0.81) or between males and females (X^2 = 0.066, 1 df, P = 0.77). Males and females each ingested 46 tags, males passed 10 and females passed 9.

It seems unlikely that tags would pass through different size digestive tracks at the same rate. This indicates that some tags were eliminated by other means. Rootes (unpublished data) found nutria (Myocostor coypus) to be the principle food of alligators in Lacassine Pool. Nutria remains occurred in 47% of 123 alligator stomachs collected during the 1986 harvest. Web tags retrieved from stomachs collected during 1987 and 1988 were occasionally found bound in tightly compacted nutria hair balls. If hair balls were regurgitated, some tags may have been passed orally.

Of 92 tags ingested, 79.3% were retained after 39.7 $\pm$ 3.6 (mean $\pm$ SD) days (Table 2). In all cases, at least 1 of the 2 tags ingested was retained; therefore, predation of a tagged animal would have been identified. If the probability of retaining a tag is

assumed to be a constant 0.79 during each successive 40-day period, the probability a web tag would be retained in an alligator's stomach after 6 months would be 0.35 and the probability of retaining a tag 1 year would 0.12.

Chabreck (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. Six months would elapse between the resumption of normal feeding activity and the end of the fall harvest. With an expected 35% retention rate after 6 months, at least 1 of the 3 web tags on a marked alligator eaten immediately after the resumption of normal feeding activity would likely be retained in a predator's stomach at harvest. Conversely, all tags ingested during the one month before the end of the normal feeding the previous fall, may have been eliminated.

Calculations of cannibalism mortality are based on the assumption that web tags recovered from stomachs represent all cannibalism of marked alligators occurring during the 12 months prior to harvest. Undoubtedly some cases have been missed. Likewise, possibly a few tags from age 11 months and older alligators were retained over 1 year. All hatchlings were tagged 12 months prior to the 1988 harvest. Calculations based on the above assumption should provide minimum cannibalism mortality rates.

Alligator Population Estimate

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

Of the 931 alligators sighted during 1988 night counts, 15.5% were adults. Twenty-nine and nine tenths percent of the adult females in Lacassine Pool nested in 1988 (Chapter 3). Of the 1,009 adult alligators harvested from the pool between 1983 and 1988, 38.9% were females. Dividing total nests by AFE (0.155x0.299x 0.389) yields a July 1988 population estimate of 14,868 alligators.

Cannibalism Mortality in Hatchling Alligators

Web tags from 5 of the 131 hatchling alligators marked in September 1987 were recovered from stomachs of alligators harvested in September 1988. Of the estimated 5,026 harvestable size alligators in the pool (Table 3), stomachs from 453 were examined (Table 1). Dividing 5 by the proportion of total predator alligators sampled (0.09) yields a marked hatchling loss of 55. If unmarked hatchlings were cannibalized at the same rate as marked, 42.0% of all hatchlings were lost to cannibalism during the first year of life. Carbonneau (1987) estimated total hatchling mortality in Lacassine Pool to be 83.6% by age 1 year. Based on this estimate, 50.2% (0.836 x 0.42) of total hatchling mortality would be attributable to cannibalism.

Cannibalism Mortality in Older Alligators

A total of 3,670 alligators were cannibalized from September 1987 through August 1988 (Table 4). Assuming constant recruitment and age specific mortality rates, cannibalism mortality was 24.7% of the standing crop.

Total mortality by size class of alligators 11 months and older (Table 5) was calculated based on the assumption that recruitment and age specific mortality rates were constant. Total mortality for all size classes was 5,164 or 35.1% (5,164/14,868) of the standing crop (Table 5). Based on this estimate, cannibalism accounted for 71.1% of total mortality of age 11 month and older alligators.

Although cannibalism accounted for a substantial portion of total mortality, prey alligators comprised an insignificant portion of each predator's diet. An estimated 5,026 potential predators (alligators > 1.20-m, Table 3) were in the July 1988 population. Predators cannibalized an estimated 3,670 alligators age 11 months and older (Table 4) during the year ended 31 August 1988 or 0.73 prey per predator in the standing crop per year.

Carbonneau (1987) estimated that 23.8 alligators were hatched per nest counted during aerial surveys of Lacassine Pool in 1986. Applying this rate to 704 nests counted in 1987 (Carbonneau 1987), 16,744 hatchlings would have been available to predators in September 1987. With a 42.0% cannibalism mortality rate, an estimated 7,037 hatchlings would have been cannibalized by predators during the year ended 31 August 1988 or 1.4 hatchlings per predator in the standing

crop per year. Total cannibalism of all size classes of prey alligators would have been 2.13 prey per predator alligator in the standing crop per year.

Size of Prey Compared to Size of Predator

Simple linear regression was used to relate total length of predator alligators to total length of their cannibalized prey. Prey alligators were assumed to have been cannibalized 6 months prior to the predator's harvest or on the date they were tagged, whichever occurred last. Growth of alligators marked more than 6 months before the predator's harvest was projected by growth curves presented by Rootes (1989).

Data on length of prey alligator by length of predator alligator (Fig. 3) indicate a significant linear relationship between the two ($n = 72$, $R^2 = 0.608$; slope different from zero at $P < 0.001$). Only 3 of the 30 prey alligators cannibalized by predators > 2.73 m TL were < 1.0 m TL. If these three outlying points are dropped from analysis, R^2 increases to 0.704.

All marked hatchlings (n=5) were cannibalized by alligators < 1.78 m TL. Mean prey size was 0.53 $\pm$ 0.18 m (n=28) for 1.21-2.12 m TL predators, 1.06 $\pm$ 0.40 m (n=13) for 2.13-2.73 m TL alligators, and 1.49 $\pm$ 0.42 m (n=31) for predators over 2.73 m TL.

Based on the regression equation, alligators would not be immune from cannibalistic attacks until they reached a TL of approximately 2.13 m, assuming a maximum predator size of 4.0 m (Rootes 1989). Web tags from 4 alligators approximately 2.13-m long were recovered from

stomachs. All three web tags from a 2.08-m male tagged in May 1988 were recovered from the stomach of a 2.85 m male harvested in September 1988. Although the difference in total length of these animals was not large, the difference in weight was substantial. Based on weight to length curves developed from alligators harvested in Lacassine Pool (Joanen et al. 1989), a 2.08 m TL alligator would be expected to weigh approximately 25 kg while one 2.85 m TL would weigh 77 kg.

If a total length of 0.2 m at hatching is assumed, a minimum predator size of 1.35 m would be expected from the regression. No tags were recovered from alligators less than 1.40 m TL (n=27). This tends to support the assumption that only harvestable size alligators are cannibalistic.

Sex Ratio of Prey

The sex ratio of prey alligators did not differ from the sex ratio of the general population ($\underline{X}^2 = 0.431$, 1 df, P = 0.52). Sixty-three percent of 4,610 alligators captured during the refuge's tagging program were males. Sex was known for 43 of the prey alligators; 60.1% were males. Prey cannibilized by male predators were 61.1% males (n=36), and prey of female predators were 57.1% males (n=7).

DISCUSSION

Cannibalism among alligators in Lacassine Pool appears to be a major population regulating mechanism, accounting for more than 50%

of total mortality. How this relates to other populations 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). Usually the effects of high density are confounded with those of food shortages. Decreasing food availability would likely increase foraging activity, lower attack thresholds, expand diets beyond normal limits, and leave animals deprived of food weakened and increasingly vulnerable to cannibalism (Polis 1981). Low growth rates (Chapter 2), poor weight-length ratios (Joanen et al. 1989), and high densities (McNease and Joanen 1978) relative to other Louisiana alligator populations indicate Lacassine Pool is an extreme case. However, density estimates from night count data collected in other areas of the Southeastern U.S. suggest that at least the density factor in Lacassine Pool is comparable to some other unharvested populations (Chabreck 1985). This possibly indicates cannibalism intensity is high in these populations as well.

Two additional factors could contribute to the intensity of cannibalism behavior in Lacassine Pool. The pool is surrounded by a 2 m high, 10 m wide levee. To what extent this interferes with normal dispersal of both predator and prey alligators is unknown. At least some dispersal has occurred. Over 100 alligators tagged in Lacassine Pool were recovered outside the levee system between 1982

and 1988. All alligators were recovered by baited hooks during the annual harvest season. The smallest alligator recovered was 1.26 m TL.

The habitat available in Lacassine Pool may also be a factor relating to cannibalism. Three general habitat types occur: maidencane-bulltongue stands, ponds, and canals. These three habitat types are well-interspersed in relatively small blocks. This may bring different size alligators, which normally inhabit different habitats (Lang 1987) into closer contact.

Although large males (> 2.73 m TL) were 5 times more cannibalistic than smaller harvestable size alligators, they made up a relatively small part (2%, Table 3) of the total population. As a result, they accounted for only 19.9% (Table 4) of total cannibalism. These larger animals preyed principally on large juveniles and small adults (1.21-2.12 m TL), avoided hatchlings completely, and took very few age 11 month and older alligators < 1.21 m TL.

Several factors could account for the absence of hatchlings through medium size juveniles (0.24-1.20 m TL) in the diets of large males. The energy gained by cannibalizing a small juvenile may not be worth the energy expended to capture it. Habitat partitioning by different size alligators could reduce the chance of encounters between large males and small juveniles. Also, large males may not perceive small juveniles as potential competitors.

The size relationship between predator and prey alligators, the relative abundance of each size class in the population, and the fact

males and females were cannibalized in the same proportion that they occur have important implications for the way the population size structure was regulated. Large males accounted for 19.9% of total cannibalism cases and preyed on cohorts that represent 23% (Table 3) of the standing crop. Medium size predators (2.13-2.73 m TL) accounted for 23% of the cannibalism cases and preyed principally on medium size juveniles (0.75-1.20 m TL) which comprised 25% of the standing crop. Small predators (1.21-2.12 m TL) accounted for 57% of the total cases of cannibalism and preyed on small juveniles (0.35-0.74 m TL) which comprised 46% of the standing crop. This suggest that cannibalism mortality results in a relatively uniform reduction among all cohorts in the 0.35-2.12 m TL group, insuring no one cohort is either eliminated or becomes dominant. This could have a stabilizing effect on future populations by insuring reduced but relatively uniform recruitment into the larger adult group (> 2.12 m TL).

Large home ranges (Joanen and McNease 1973) and a more aggressive nature (Gugyisberg 1972) indicate 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 resulting in increased prey availability to survivors, cannibalism behavior in alligators would enhance group 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.

Distribution of cannibalism over a range of size classes instead of concentrating on the very smallest individuals may improve population energetics. Polis (1981) points out that when food is limiting to adults, cannibalism can serve as an energy loop, which maintains calories in a population, particularly when immature animals feed on resources that are inaccessible or underutilized by adults. Studies indicate that small juvenile alligators prey principally on insects and small minnows, medium size juveniles depend more on crustaceans, and large juveniles and adults depend more on larger fish, birds, and mammals as growth occurs (Giles and Childs 1949; Fogarty and Albury 1967; Chabreck 1971; and Delany and Abercrombie 1986). By distributing cannibalism over a variety of prey sizes, predator alligators in Lacassine Pool may have become more efficient in indirectly expanding their prey base.

Cannibalistic behavior improves individual fitness several ways (Alexander 1974, Bertram 1975, Sherman 1980, and Polis 1981). Potential resource competitors with the cannibal and its offspring are eliminated. Potential intraspecific predation on the cannibal's offspring is reduced. Also, cannibals increase their relative reproductive output by eating their rival's parental investment. Cannibalism would become disadvantageous if an individual destroyed its own protengy faster than those of its conspecific competitors (Fox 1975).

Cannibalism among alligators in Lacassine Pool appears to be functioning as a means of interference competition, 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, relative prey availabilities, and habitats should be examined.

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Figure 1. Location of the study area, Lacassine National Wildlife Refuge

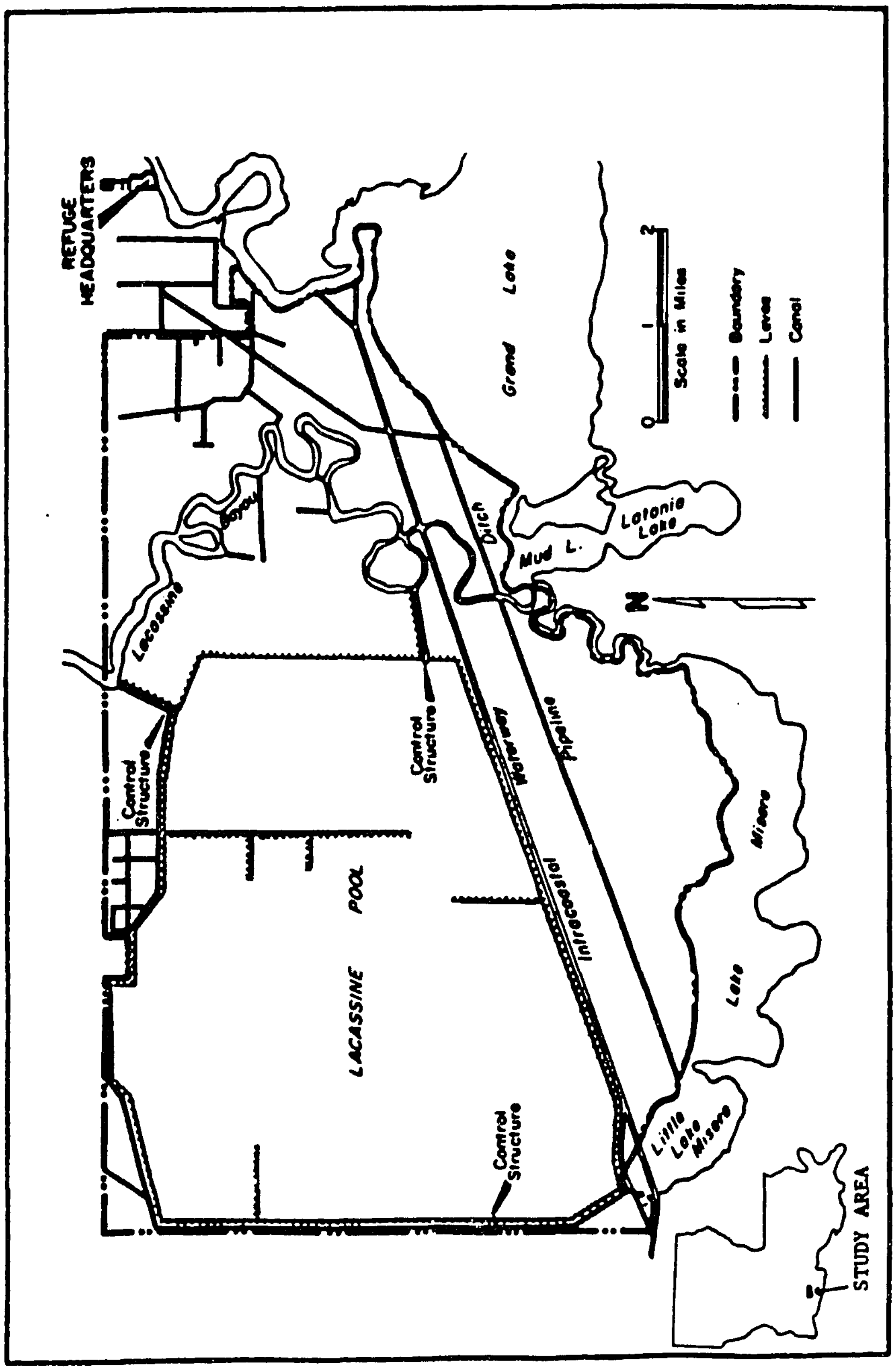

REFUGE
HEADQUARTERS
Grand Lake
Lacassine
Bayou
Mud L.
Lotonie
Lake
Ditch
Pipeline
Intracoastal Waterway
Control
Structure
Control
Structure
Control
Structure
LACASSINE POOL
Little
Lake
Misere
Misere Lake
N
0 1 2
Scale in Miles
Boundary
Levee
Canal
STUDY AREA

Figure 2. Index of cannibilism by size class, and sex of predator alligator, Lacassine Pool, 1987 and 1988.

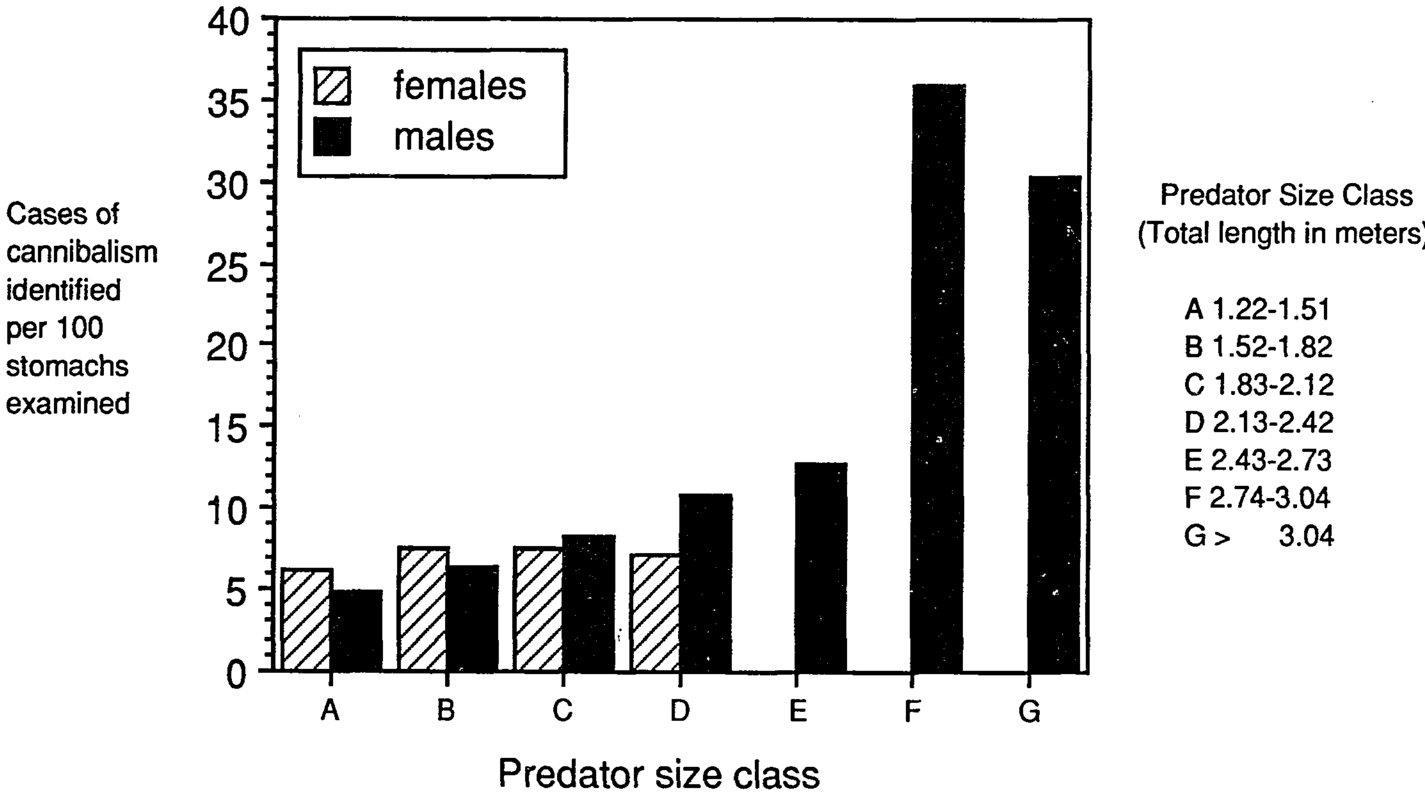
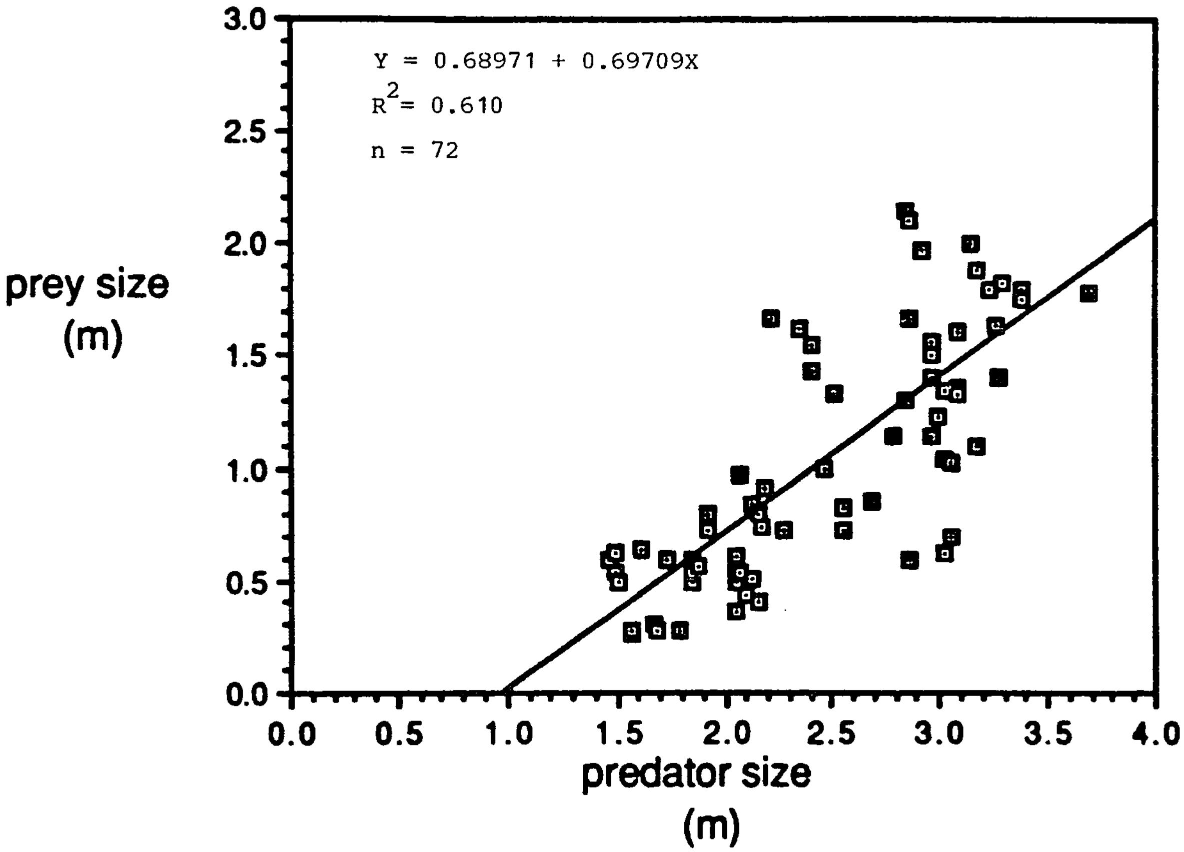

Cases of cannibalism identified per 100 stomachs examined
0
5
10
15
20
25
30
35
40
females
males
A
B
C
D
E
F
G
Predator size class
Predator Size Class
(Total length in meters)
A 1.22-1.51
B 1.52-1.82
C 1.83-2.12
D 2.13-2.42
E 2.43-2.73
F 2.74-3.04
G > 3.04

Figure 3. Relationship between total length of predator alligators and total length of prey alligators, Lacassine Pool, 1987 and 1988.



Y = 0.68971 + 0.69709X
R2 = 0.610
n = 72
prey size (m)
predator size (m)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0

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

Predator total length (m)	1987		1988		Combined years	
	Number of stomachs examined	Cases of cannibalism identified	Number of stomachs examined	Cases of cannibalism identified	Number of 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

Table 2. Retention of web tags in the digestive system of harvestable size alligator taken from Lacassine Pool, 1988.

Total length of alligator (m)	Tags ingested	Tags retained	Percent passed	Days elapsed Mean	SD
1.22-1.82	22	17	22.7	41.3	2.14
1.83-2.12	36	29	19.4	39.2	2.80
2.13-2.42	16	14	12.5	40.1	3.43
2.43-2.73	10	7	30.0	37.8	4.60
> 2.73	8	6	25.0	39.8	3.34
Total	92	73	20.7	39.7	3.60

Table 3. Estimate of July 1988 alligator population, Lacassine Pool, 1988.

Total length of alligator (m)	Percent of total alligators sighted during night counts[a]	July 1988 alligator population
< 0.92	48.2	7,166
0.92-1.20	18.0	2,676
1.21-1.51	9.8	1,467
1.52-1.82	8.5	1,264
1.83-2.12	6.0	892
2.13-2.42	5.6	833
2.43-2.73	1.9	282
2.74-3.04	1.1	164
> 3.04	0.9	134
Total	100.0	14,868[b]

[a] A total of 931 alligators were counted during 1988 night counts.

[b] As determined from nest counts.

Table 4. Cannibalism of age 11 months and older alligators, Lacassine Pool, 1988.

(A) Total length of predator alligator (m)	(B) Cases of cannibalism identified[a]	(C) Percent of predators sampled[b]	(D) Percent of population marked[c]	(E) Total cases of cannibilism[d]	(F) Percent of total cannibalism cases
1.21-1.51	2	3.2	12.9	484	13.2
1.52-1.82	9	7.3	12.9	955	26.1
1.83-2.12	12	14.2	12.9	655	17.8
2.13-2.42	7	11.0	12.9	493	13.4
2.43-2.73	5	11.0	12.9	352	9.6
2.74-3.04	13	21.3	12.9	473	12.9
> 3.04	7	21.0	12.9	258	7.0
Total	55	N/A	N/A	3,670	100.0

a/ From stomach content analysis (Table 1).

b/ $\frac{\text{Number of Stomachs Analyzed in Size Class (Table 1)}}{\text{Pre-harvest Population in Size Class (Table 3)}}$

c/ As determined from recapture rates experienced during 1988 tagging and harvest programs.

d/ $\frac{\text{Column B}}{\text{Column C x Column D}}$

Table 5. Total annual mortality of alligators age 11 months and older, Lacassine Pool.

Size class (m)	Total number in size class[a]	Mean age of individuals in size class (months)[b]	Reduction from previous size class	Time elapsed (months)	Annualized mortality
< 0.92	7,166	18	N/A	N/A	N/A
0.92-1.20	2,676	34	4,490	16	3,367
1.21-1.51	1,457	47	1,219	13	1,125
1.52-1.82	1,264	62	193	15	154
1.83-2.12	892	81	372	19	234
2.13-2.42	833	101	59	20	35
2.43-2.73	282	134	551	33	200
2.74-3.04	164	169	118	35	40
> 3.04	134	209	29	41	9
Total	14,868	N/A	N/A	N/A	5,164

[a]From Table 3.

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

CHAPTER TWO

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RH: ALLIGATOR GROWTH RATES · Rootes

A COMPARISON OF GROWTH RATES AND WEIGHT-LENGTH RELATIONSHIPS OF AMERICAN ALLIGATORS ON TWO LOUISIANA MARSHES.

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Abstract: Growth rates and weight-length relationships of alligators (*Alligator mississippiensis*) on Rockefeller Refuge and Lacassine National Wildlife Refuge (NWR) were compared. Both refuges are located in southwestern Louisiana and are composed mostly of marshlands. Rockefeller Refuge is principally a saline marsh and Lacassine NWR is a fresh marsh. Male alligator growth rates on both areas were greater than female rates ($P < 0.0001$). Growth rates of males and females were greater on Rockefeller Refuge than on Lacassine NWR ($P < 0.0001$). Males on Rockefeller Refuge reached the TL of sexual maturity (1.83 m TL) at about 6 years of age compared to 10 years of age for males on Lacassine. Females on Rockefeller Refuge reached the TL of sexual maturity (Joanen 1969) at about 7.5 years of age versus 13 years of age for females at Lacassine NWR. Males and females within both refuges grew at comparable rates up to 1.0 m total length (TL). Alligators on Rockefeller Refuge reached 1.0 m TL at about 2.5 years of age. Alligators on Lacassine NWR did not reach 1.0 m TL until age 4.5 years. Weight-length ratios of

alligators on Lacassine NWR were less than those on Rockefeller Refuge ($P < 0.0001$), suggesting that nutrition may be a factor. Based on this information, age specific fecundity and survivorship rates of alligators on Lacassine NWR were expected to be substantially lower than those of alligators on Rockefeller Refuge.

Key Words: American alligator, *Alligator Mississippiensis*, growth, weight-length ratios, fecundity, survival

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Growth rates of American alligators have been reported by several authors (McIlhenny 1934, Bara 1972, Hines et al. 1968, Kellogg 1929, and Chabreck and Joanen 1979). Computations of growth rates were mostly based on a small number of observations or on animals of limited genetic variability. Chabreck and Joanen (1979) reported growth rates based on a sample of 304 alligators marked and subsequently recaptured on Rockefeller Refuge. Rockefeller Refuge is located in southwestern Louisiana and is composed of coastal marshlands with water salinity ranging as high as 18 ppt. Much of the alligator habitat in Louisiana is freshmarsh (Joanen and McNease 1979), but no in-depth studies have been conducted on alligator growth in that habitat type. The purpose of this study was to compare growth of alligators in saline habitats as reported by Chabreck and Joanen (1979) to those of alligators in freshwater habitat. Weight-length relationships and the densities of alligators in the 2 habtitats were also compared.

STUDY AREAS

Rockefeller Refuge consists of 38,000 ha of coastal marshland and lies adjacent to the Gulf of Mexico. The area contains numerous bayous, canals, and shallow ponds. Although water salinity varies throughout Rockefeller Refuge, most alligators were captured in areas with water salinities of 5 ppt or less.

The area selected for study of growth in freshwater habitat was Lacassine National Wildlife Refuge (NWR), which is located approximately 20 km inland from Rockefeller Refuge. A 6,478 ha permanently flooded impoundment located within Lacassine NWR served as the principle study site. The impoundment, referred to as Lacassine Pool, consists of floating freshwater marsh interspersed with shallow ponds, canals, and ditches. Open water areas range from 0.3-1.0 m deep and contain submerged and floating plants. Rainfall constitutes the only source of water to the pool. Excess water is allowed to escape via 3 spillways located along the impoundment's perimeter levees.

Rockefeller Refuge was established in 1927, and alligator hunting was prohibited on the Refuge after 1943. Several hundred alligators (mostly immature and sub-adult animals) were captured on the refuge during the 1960's and relocated to underpopulated areas of the state. Only a small number of experimental and nuisance animals were removed from the population after the 1960's. From the inception of Lacassine NWR in 1937 through 1982, alligator hunting on the refuge was prohibited. Beginning in 1983 an annual commercial

alligator harvest was initiated on Lacassine Pool. Between 1983 and 1987, 753 alligators were harvested from the pool. The alligator populations on both refuges were thought to be at or near carrying capacity during the time data for this study were being collected.

METHODS

Between 1959 and 1976, approximately 2,500 alligators were captured on Rockefeller Refuge by methods described by Chabreck (1963). The total length (TL) of each animal was measured along its dorsal surface and the sex of most animals > 0.45 m TL was determined by cloacal examination (Chabreck 1963). Each alligator was marked by attaching a numbered monel tag to its dorsal tail scutes. During the study, 304 marked alligators ranging in size from 0.30 m to 3.6 m TL were recovered. Upon recovery, the total length of each alligator was measured and its sex was checked by cloacal examination. In addition to TL and sex, the weights of 222 alligators captured during the study were determined. The TL of alligators that were weighed ranged from 0.95 m to 3.51 m.

Each year between 1981 and 1988 approximately 600 alligators were captured on Lacassine Pool by methods described by Chabreck (1963). The TL of each alligator was measured along its dorsal surface and the sex of most animals > 0.45 TL was determined by cloacal examination (Chabreck 1963). Each alligator was marked with 3 like-numbered monel web tags. One tag was attached to the webbing of each hind foot and one tag was attached to the webbing of a front

foot. A total of 441 marked alligators ranging in size from 0.45 m to 3.58 m TL were recovered during the study.

Upon recovery the TL of each alligator was measured and its sex was checked by cloacal examination (Chabreck 1963). The weight, TL, and sex of 249 alligators harvested from the pool in 1988 were obtained from Joanen et al. (1989). The TL of these alligators ranged from 0.97 m to 3.60 m.

The von Bertalanffy growth curve (von Bertalanffy 1960) was used as a model to compute growth in TL with time:

$$x = a\ (1 - be^{-kt})$$

where x is TL, t is age, b is TL at birth, and a and k are parameters to be estimated. A derivation of the model presented by Fabens (1965) was used to accommodate the capture-recapture data:

$$y = x + (a - x)\ (1 - e^{-kd})$$

where x = initial TL, y = TL at recapture, and d = time lapse between x and y.

Chabreck and Joanen (1979) noted that alligators in southern Louisiana do not feed, and presumably do not grow during winter dormancy, approximately November through February. Therefore, computations of d were adjusted for an 8-month growing season. Based on measurements of several hundred individuals, TL of newly hatched alligators (b) from both areas was determined to be 0.24 m. The unknown parameters (a and k) were estimated by the least squares method using PROC NLIN (SAS Institute, Inc. 1985). To confirm the accuracy of the estimates made by PROC NLIN, the values of a and k

were recomputed with a FORTRAN program presented by Fabens (1965). Partial F tests were used to compare growth curves by refuge and sex of alligators.

The weight-length relationship in alligators was assumed to fit the model:

$$W = aL^b$$

where W = weight in kg, L = TL in m, and a and b were coefficients to be estimated. The model was transformed to a linear function for analysis:

$$\log W = \log a + b \log L.$$

Simple linear regression techniques were applied on the transformed data to provide statistical inferences. Comparisons between refuges were made by t-tests and comparisons between male and female alligators were made by partial F tests (Steel and Torrie 1980). PROC NLIN (SAS Institute, Inc. 1985) was used on non-transformed data for final parameter estimates.

RESULTS

Male and female alligators captured on Lacassine Pool grew at different rates ($F = 37.68$; 2, 437 df; $P < 0.0001$) (Fig. 1). Estimated values for the von Bertalanffy model were:

$$\text{Males:} \quad x = 3.65\ (1 - e^{-0.0078t})$$

$$\text{Females:} \quad x = 2.39\ (1 - e^{-0.0128t})$$

These equations accounted for 97% of the variation in TL of males and 92% of the variation in TL of females. Maximum expected lengths of males and females on Lacassine Pool were 3.65 m TL and 2.39 m TL,

respectively. The asymptotic 95% confidence intervals were 3.34 - 3.95 m TL for males, and 2.18 - 2.60 m TL for females.

Males and females grew at comparable rates up to a TL of about 1.0-m, reaching this size at 4.5 years of age. After a TL of 1.0-m was reached, female growth rates declined at a faster rate than males. Based on the growth curves, males reached sexual maturity (1.83 m TL) at about 10 years of age, and females reached maturity at about 13 years of age. At age 10 males were growing 42% faster than females, and by age 20 the male growth rate was 350% greater than that of females. After age 20, the male growth rate declined rapidly. The expected TL of males on Lacassine Pool at ages 20 and 30 were 2.70 m and 3.10 m, respectively.

Males and females captured on Rockefeller Refuge also grew at different rates ($\underline{F} = 56.11$; 2, 302 df; $P < 0.0001$) (Fig. 1). Calculated values for the von Bertalanffy models were:

$$\text{Males:} \quad x = 4.23\ (1 - e^{-0.01068t})$$

$$\text{Females:} \quad x = 2.74\ (1 - e^{-0.01972t})$$

These equations accounted for 96% and 91% of the variation in growth of males and females, respectively. Maximum expected lengths of males and females on Rockefeller Refuge were 4.23 m TL and 2.53 m TL, respectively. The asymptotic 95% confidence intervals of TL were 3.86 - 4.60 m for males and 2.48 - 2.97 m for females.

As with alligators in Lacassine Pool, males and females at Rockefeller Refuge grew at comparable rates up to a TL of 1.0 m, but reached this size at approximately 2.6 years of age. Data indicated

males were expected to reach sexual maturity at about age 6, and females reached maturity at approximately 7.5 years of age. At age 10, the male growth rate was 62% greater than the female's rate, and by age 20 male growth rates were twice that of females. After age 20, male growth rates declined. A 20 year old male on Rockefeller Refuge was expected to be 3.50 m long, and at age 30 males reach 3.90 m TL.

Growth of males on Rockefeller Refuge was different than that of males on Lacassine Pool (F = 166.48; 2, 451 df; $P > 0.0001$) (Fig. 1). Growth rates apparently differed from the time the animals were hatched. Males were expected to reach 1.0 m TL on Rockefeller Refuge in 2.5 years and on Lacassine Pool in 4.5 years. Rockefeller males were expected to obtain sexual maturity 4 years sooner and grow to a greater TL than males on Lacassine Pool.

Growth rates of females on Rockefeller Refuge also differed from that of females on Lacassine Pool (F = 47.64; 2, 288 df; $P > 0.0001$) (Fig. 1). Females on Rockefeller Refuge were expected to obtain sexual maturity 5.5 years sooner than females on Lacassine Pool, and would reach a greater TL. The variation in growth rates among individual alligators on Rockefeller Refuge was higher than the variation in growth rates among individuals on Lacassine Pool (F = 2.37; 302, 437 df; $P < 0.01$).

Male and female alligators harvested from Lacassine Pool had the same weight-length relationship (F = 1.59; 2, 2.45 df; $P < 0.204$). The same was found for males and females captured on Rockefeller

Refuge ($\underline{F}$ = 0.20; 2, 220 df; P < 0.82). Male and female data within the area were pooled to make comparisons between areas.

No difference was found in the slopes of the weight-length regression lines of alligators taken from the two areas ($\underline{t}$ = 0.77, 469 df, P = 0.44). The intercepts were, however, different ($\underline{t}$ = 7.86, 469 df, P < 0.0001). This suggests that alligators on Lacassine Pool were thinner than those on Rockefeller Refuge. Calculated values for the weight-length model were:

Lacassine: $W = 1.86L^{3.593}$

Rockefeller: $W = 2.84L^{3.342}$

These equations accounted for 97% and 98% of the variations in weight-length ratios of alligators on Lacassine Pool and Rockefeller refuge, respectively. The variation in weight-length ratios among individual alligators on Rockefeller Refuge was higher than the variation in ratios among individuals on Lacassine Pool.

Alligators harvested from Lacassine Pool had lower weight-length ratios than the alligators captured on Rockefeller Refuge (Figs. 2 and 3). A 1.0-m TL alligator harvested from Lacassine Pool was expected to weigh 1.9±1.2 kg (95% confidence limits). A 1.0-m TL alligator captured on Rockefeller Refuge was expected to weigh 2.8±1.2 kg. Expected weights of 2.0-m TL alligators on Lacassine Pool and Rockefeller Refuge were 22.5±1.3 kg and 28.8±13 kg, respectively. A 3.0-m TL alligator on Lacassine Pool was expected to weigh 111.8±1.5 kg. This indicates that a 1-m TL alligator on Rockefeller Refuge weighed 47.4% more than a comparable size

alligator on Lacassine Pool. While 2.0-m and 3.0-m TL alligators weighed 28.0% and 16.0% more, respectively.

DISCUSSION

The maximum lengths projected by the von Bertalanffy model correspond quite well to what was actually seen on refuges. The maximum TL projected for male alligators on Rockefeller Refuge was 4.2 m. During the study 2 alligators approaching that length were observed on the refuge. The maximum TL of female alligators on the Rockefeller Refuge was projected to be about 2.74 m, and several females approaching that length were captured.

Of 860 adult male alligators harvested from Lacassine Pool between 1983 and 1989, the largest had a TL of 3.66 m. The projected maximum TL for male alligators was 3.65 m. The model slightly underestimated the maximum TL for female alligators on the pool. The maximum TL for females was projected to be 2.39 m. Of the 356 adult females harvested during the study, 4.5% were longer than 2.39 m. The largest female harvested was 2.59 m long; however, this length was within the asymptotic 95% confidence limits.

The difference in growth rates and projected maximum total lengths of alligators on the two areas have important implications for the populations' relative reproductive capacities and survivorship rates. Female alligators on Lacassine Pool required 73% longer to reach sexual maturity. Wilkerson (1985) and Taylor et al. (1987) found that clutch size and the probability an adult female will nest

increased as the size of the female increased. Once reaching sexual maturity, female alligators on Lacassine Pool were slower to grow into the larger adult size classes and reached a shorter maximum total length. All of these factors suggest the age specific fecundity rates of females on Lacassine Pool were dramatically lower than those of females on Rockefeller Refuge.

Nichols et al. (1976) pointed out that survivorship in sub-adult alligators was a function of size. Survivorship rates were lowest in alligators < 0.45 m TL, and gradually increased as the size of the alligator increased. Alligators on Rockefeller Refuge reached 1.0 m TL about 2 faster than alligators on Lacassine Pool. Because sub-adults on Lacassine Pool were in the more vulnerable size classes much longer, age specific survivorship rates were likely to be lower than the survivorship rates of alligators on Rockefeller Refuge.

The lower weight-length ratios of alligators on Lacassine Pool indicated relative prey availability on the pool was less than that on Rockefeller Refuge. Although no controlled studies were done with reptiles, Shilo and Sarig (1989) reported that growth rates and maximum weight-length ratios varied among different genetic strains of warm water fishes. Because of the proximity of the two study areas, and the movement capabilities of alligators (Chabreck 1965), it is unlikely that genetics played a role in this study. Two alligators tagged on Lacassine Pool were subsequently recaptured within 1.0 km of Rockefeller Refuge.

The lower variability among individual alligators on Lacassine Pool in both growth rates ($P < 0.01$) and weight-length ratios ($P < 0.05$) may also be the result of nutrition. If food was more available to alligators on Rockefeller Refuge, genetically superior individuals may have been released to reach their full potential. Whereas on Lacassine Pool, food deprivation may have suppressed such a response.

No direct measurements of the prey base available to alligators on the 2 areas were made during these studies; however, several factors suggest prey availability would have been greatest on Rockefeller Refuge. Gosselink et al. (1979) estimated that the primary production of intermediate marshes in the Gulf Coast was almost twice the primary production in fresh marshes. Rainfall constitutes the only source of water to Lacassine Pool. The marshes in Rockefeller Refuge are subjected to both tidal fluctuations and inland runoff. Both seawater and runoff would have added nutrients (Chabreck 1988) to the Rockefeller system. A number of the prey species available to alligators on Rockefeller Refuge (Chabreck 1971) were not available to alligators on Lacassine Pool. Blue crab (*Callinectes sapidos*), fiddler crabs (*Uca pugnax*), Striped mullet (*Mugel cephalus*), menhaden (*Brevoortia patronus*), and croaker (*Micropogan undulatus*) were available in great quantities to alligators on Rockefeller Refuge but were not available to alligators on Lacassine Pool.

Joanen and McNease (1987) reported that alligator nest densities on the portion of Rockefeller Refuge where growth and weight-length data were collected were 1 nest per 7.6 ha. Alligator nest densities on Lacassine Pool were 1 nest per 22.3 ha in 1988 (Chapter 1). Joanen and McNease (198) reported that approximately 60% of the adult females on Rockefeller Refuge nest annually. About 30% of the adult females on Lacassine Pool nested in 1988 (Chapter 3). After adjusting for the portion of adult females that nested, adult female alligator densities were 1 female per 4.6 ha on the intensive study area in Rockefeller Refuge and 1 female per 6.7 ha on Lacassine Pool. This indirectly suggests that alligator densities on that portion of Rockefeller Refuge where growth data were collected were higher than those on Lacassine Pool.

Differences in growth rates, weight-length ratios, and densities between alligators on Rockefeller Refuge and alligators on Lacassine Pool suggest that estuarine marsh provides better alligator habitat than fresh marsh. Also, the effect of prey availability on growth may partially regulate alligator populations through decreased fecundity and survivorship rates.

Both age specific fecundity and survivorship rates are important components in any population model. The great disparity in growth found in this study, along with the possibility of genetic effects in geographically distinct populations, suggest the use of generalized rates in alligator population models are inappropriate.

Considerable difference was found between the 2 areas in the growth rates of smaller sub-adult alligators (< 1.0 m TL). The parallel nature of the weight-length regression lines of alligators from the 2 areas indicate that the pattern of lower weight-length ratios in alligators on Lacassine Pool was established when the animals were < 1.0 m TL. Thusfar, all food habit studies of sub-adult alligators (Giles and Childs 1949, Fogarty and Albury 1968, and Chabreck 1971) have been based an alligators > 1.0-m TL. Because the growth of young alligators (< 1.0 m TL) can greatly effect survivorship and the age specific fecundity rates of the population, the food requirements and availability to these animals needs to be better understood.

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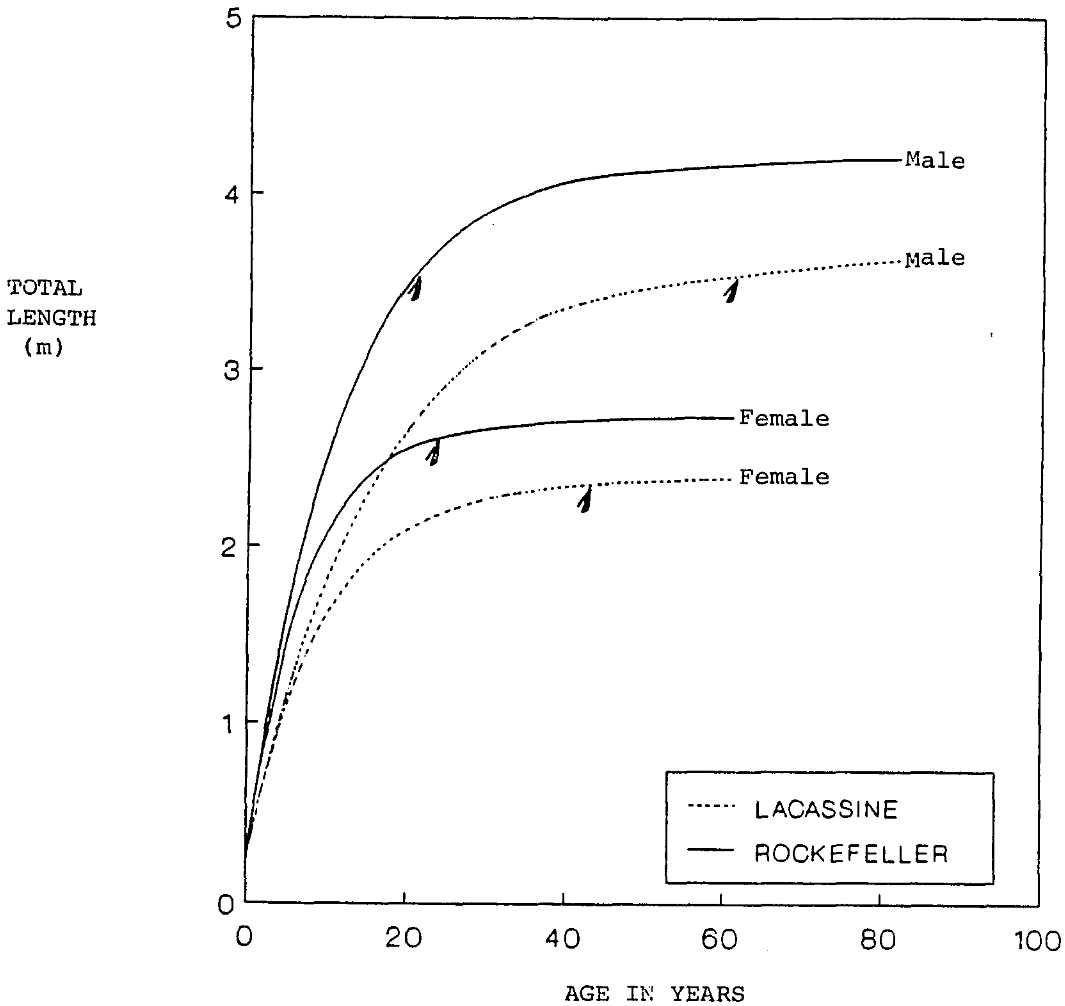
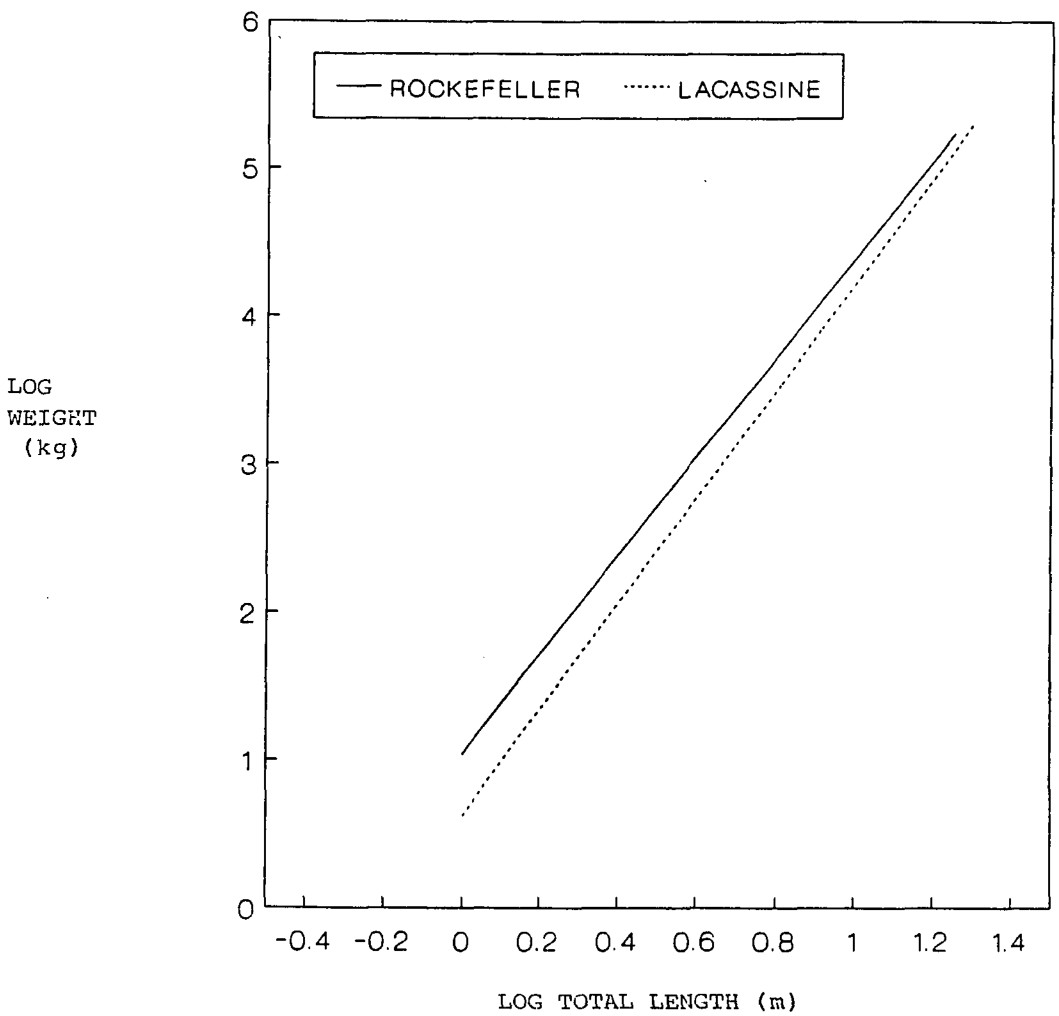
Figure 1. Length-age relationship derived from capture-recapture data, Rockefeller Refuge 1959-1976 and Lacassine Pool 1981-1988.



- Limit of actual data

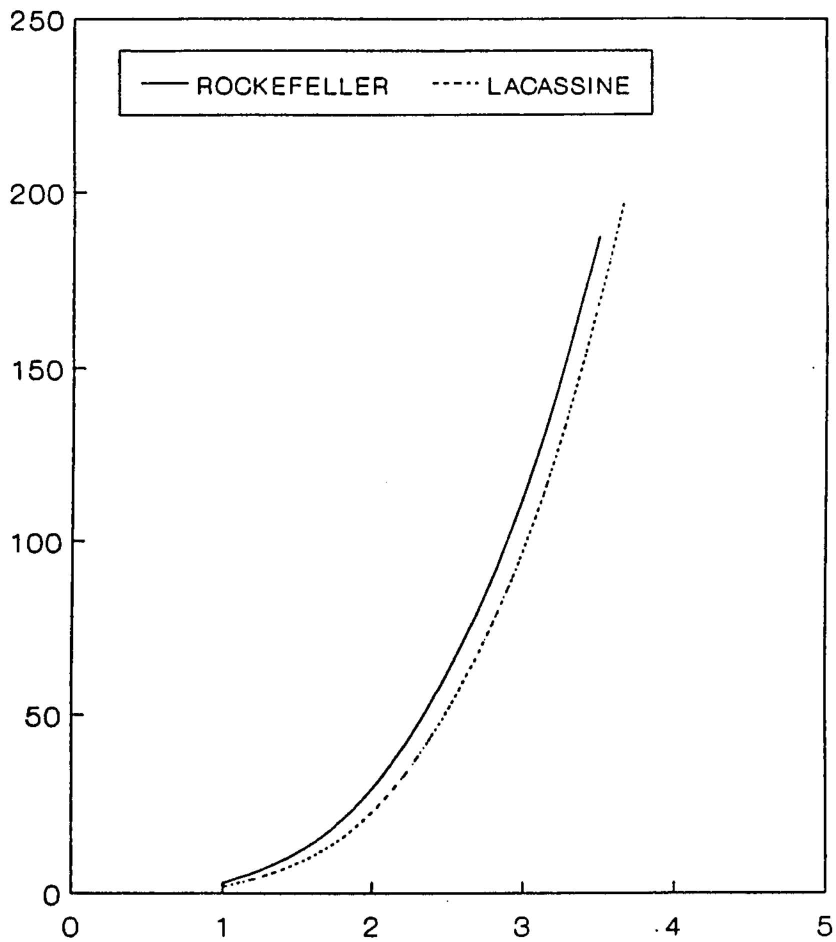
Figure 2. Log weight-length relationship of alligators taken from Rockefeller Refuge 1959-1976 and Lacassine Pool 1988.



NOTE: Regression lines represent the limits of actual data.

Figure 3. Weight-length relationship of alligators taken from Rockefeller Refuge 1959-1976 and Lacassine Pool 1988.

WEIGHT (kg)



TOTAL LENGTH (m)

NOTE: Regression lines represent limits of actual data.

CHAPTER THREE

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RH: ALLIGATOR HOME RANGE · Rootes

SEASONAL HOME RANGE SIZE AND MOVEMENT RATES OF ADULT FEMALE ALLIGATORS.

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Abstract: The home range size and activity pattern of adult female American alligators (*Alligator mississippiensis*) of different reproductive status were compared among seasons of the year. No difference was found during the summer nesting season in home range size ($P = 0.54$), minimum average daily movement rates ($P = 0.85$), or percent of time spent at den sites ($P = 0.51$) between nesting and non-nesting radio-collared females. Likewise, no difference ($P > 0.25$) was found in any of the three variables during the fall brooding season when radio-collared females with broods were compared to those without broods. Adult radio-collared female alligators had larger home ranges, greater minimum average daily movement rates, and spent less time at or near their den sites during the spring breeding season than any other season of the year ($P < 0.01$). Annual home range size of the 15 adult female alligators monitored during the study was 36.2 ± 42.6 (SD) ha.

Key Words: American alligator, *Alligator mississippiensis*, home range, movement rates, nesting rates

Adult female American alligator home ranges and movement rates have been studied in Louisiana and Florida (Joanen and McNease 1970, Goodwin and Marion 1979, and Taylor 1984). Joanen and McNease (1970) reported the home range size and movement rates of 4 nesting adult females occupying estuarian habitat. Goodwin and Marion (1979) and Taylor (1984) reported seasonal home ranges and movement rates of adult female alligators occupying lake habitats but made no reference to the animal's reproductive status.

Only 25 to 60% of adult female alligators nest annually in Louisiana and South Carolina; an even smaller percentage successfully hatch broods (Joanen and McNease 1980, Taylor 1984, Wilkenson 1985, and Taylor et al. 1987). To date the home ranges and movement rates of adult female alligators occupying fresh marsh habitats have not been studied; nor have comparisons been made between nesting and non-nesting females or between females with broods and those without broods. The purpose of this study was to compare the seasonal home range size and movement rates of adult female alligators of different reproductive statuses in a freshwater marsh.

STUDY AREA

The study was conducted on the 12,869-ha Lacassine National Wildlife Refuge in Cameron Parish, southwestern Louisiana. The refuge is located in the State's coastal plain, approximately 20 km inland from the Gulf of Mexico. A 6,478-ha permanently flooded impoundment located within the refuge served as the principle study site. The impoundment, referred to as Lacassine Pool, consists of floating fresh marsh interspersed with shallow ponds, lakes, and canals. Dense emergent stands of maidencane (*Panicum hemitomon*), bulltongue (*Sagittaria lancifolia*), and spikerush (*Eleocharis* spp.) dominate the marsh. Open water areas range from 0.3 - 1.0 m deep and contain submerged and floating plants including watershield (*Brasenia schreberi*), fanwort (*Cabomba caroliniana*), coontail (*Ceratophyllum demersum*), American lotus (*Nelumbo lutea*), and fragrant waterlily (*Nymphaea odorata*). Precipitation constitutes the only source of water to the pool. Excess water is allowed to escape over three spillways located along the impoundment's perimeter levees.

METHODS

Fifteen 2.05 m to 2.54 m total length (TL) female alligators were captured from an airboat between 15 April and 12 May 1988 by harpoon and cable snare as described by Taylor (1984). Two additional females were captured but not included because of transmitter failure early in the study. TL was measured along the dorsal surface of each animal. All alligators were marked with 3

like numbered monel web tags. Each alligator was fitted with a radio-transmitter (MOD-500, Telonics Inc., Mesa, Arizona) attached to a neck collar.

Lance et al. (1983) reported that plasma calcium levels were elevated between mid-April and mid-May in female alligators that were developing follicles. To determine nesting potential of radio-collared alligators, blood samples were drawn dorsally from a branch of the internal jugular as described by Wilkinson (1985). Blood was centrifuged and plasma frozen until assayed. Plasma calcium, zinc, magnesium, and iron levels were assayed as described by Lance et al. (1983).

Transmitter signal strength was checked prior to each animal's release. All alligators were released at or near the point of capture.

Two methods were used to monitor the location of each alligator. Emitted signals were followed via airboat with a TS-1/TS-2 scanner/receiver and a RA-2A hand-held 2 element "H" type yagi antenna (Telonics, Inc., Mesa, Arizona) to the animal's exact location. To minimize the likelihood of influencing the alligators' activity pattern, a maximum of 3 locations per week per animal were made by this method. Additional remote locations were made remotely by triangulation. A minimum of 3 azimuths (taken within 30 minutes of each other) were used to fix each location. Readings were made with a twin 5-beam yagi antenna mounted on a 3-m mast with a null-combiner box (Telonics, Inc., Mesa, Arizona). Telemetric error was

determined by reference transmitters at 3 known locations prior to each remote sensing session. Maximum error was $\pm 4^{o}$.

Signal transmissions were limited to approximately 50 m when alligators were submerged. When an effort was being made to track an alligator to its exact location and an initial signal was not received, ever widening circles were traveled from the animal's den until its location was found. All attempts by this method resulted in a location. No signals were received on 48% of the remote sensing attempts. In these cases, the animal was assumed to have been submerged in its previously identified home range.

Annual alligator activity was divided into 4 biological seasons: nesting (7 June - 18 August 1988), brooding (19 August - 1 November 1988), winter dormancy (1 November 1988 - 28 February 1989), and breeding (1 March - 9 June 1989). These seasons were based on the observed initiation of nest construction and egg hatching along with dormancy periods reported by Chabreck and Joanen (1979).

Reproductive status of each female was classified within seasons. All classifications were based on observations made when alligators were tracked repeatedly to their exact location. During the nesting season females were classified as non-nesting without a previous year's brood, non-nesting with a previous year's brood, or nesting. No nesting females were observed with a previous year's brood. During the brooding season alligators were classified as either with broods or without broods. Initially, females were to be classified during the breeding season as breeding or non-breeding

based on their nesting effort in June 1989. Only 2 females eventually nested. Because of sample sizes, statistical comparisons within the breeding season were not possible.

Approximately 50% of the locations made during the nesting, brooding, and breeding seasons were made at night. Less than 10% of the winter dormancy locations were made at night.

Home range size was estimated by the minimum convex polygon method (Mohr 1947) because of its robustness with autocorrelated data (Swihart and Slade 1985) and to facilitate comparisons with other studies. Adequate sample size for home range analysis was determined from area observations curves (Odum and Kuenzler 1955). Alligator activity was assessed by 2 parameters: 1) Minimum daily movement rate -- the distance between successive locations divided by the time elapsed between these locations; and 2) percent of times the female was located less than 25 m from her den.

Three habitat types were available to alligators in Lacassine Pool: maidencane-bulltongue stands, shallow ponds, and canals. These habitat types were well-interspersed in small blocks. Because of homogeneity and interspersion, analysis of habitat use was not practical.

Analysis of variance (ANOVA) was used to test for differences in home range size and alligator activity among seasons and reproductive statuses. If ANOVA showed a significant difference, a Duncan multiple range test was conducted to detect differences among all possible paired comparisons (Steel and Torrie 1980).

RESULTS

The home range size of all adult female radio-collared alligators during the nesting season was 13.7 $\pm$ 10.2 ha (mean $\pm$ SD) (Table 1). Home range size ranged from 5.9 ha to 47.1 ha. The minimum average daily movement rate for all classes was 25.1 $\pm$ 17.4 m (Table 1). Minimum average daily movement rates ranged from 5.9 m to 73.1 m.

Lance et al. (1983) found that plasma calcium levels of adult (> 1.82 m TL) female alligators exceeded 5 mM/L between mid-April and mid-May when the animals were developing ovarian follicles. Six of the 15 radio-collared females were found to have calcium levels above 5 mM/L. Of these, 5 constructed nests and deposited eggs in June 1988. One of 4 females (1.83 - 2.13 m TL) nested; 3 of 9 females (2.14 - 2.44 m TL) nested, and 1 of 2 females greater than 2.44 m TL nested. Based on these rates an estimated 29.9% of the adult female alligators in Lacassine Pool nested in 1988 (Table 1).

Pods of young alligators hatched during 1987 were repeatedly found at the dens or in the vicinity of 5 radio-collared non-nesting females in 1988. No previous years broods were sighted with radio-collared nesting females during the nesting season.

During the nesting season, no difference was found in the home range size of nesting females, non-nesting females with broods, and non-nesting females without broods ($F = 0.65$; 2, 12 df; $P = 0.54$) (Table 2). Likewise, no difference was found in the average daily movement rates among the three groups ($F = 0.17$; 2, 12 df; $P = 0.85$).

Of the fifteen radio-collared females, only 1 (a nesting female) occupied what could be classified as lake habitat (> 80% open water). The other 14 occupied marsh habitat (< 40% open water). The one lake alligator occupied a consistently larger home range through out the study, moving considerable distances in and around the edge of the lake. When this alligator was dropped from analysis, the mean home range of the remaining nesting alligators was 10.5 $\pm$ 4.8 ha.

Dens (Joanen and McNease 1970) were used consistently by all classes of females during the nesting season. Because of the error inherent in triangulation, only observations obtained by tracking signals to their exact location were used to determined the percent of time females were at or near (within 25 m) their dens. Females spent 68.6 $\pm$ 6.5% of their time at or near their dens during the summer nesting season (Table 1). No difference was found among classes of females ($F = 0.72$; 2, 12 df; $P = 0.51$). There was, however, considerable disparity between day and night readings. Females were located at or near their dens on 87% of the daytime observations, and 46% of the night observations.

Only 2 of the 5 nesting females successfully hatched broods (Table 3). To make comparisons between brooding and non-brooding female alligators, the two females with 1988 broods were combined with the 5 females that were accompanied by 1987 broods. No difference was found in home range size ($F = 1.48$; 1, 13 df; $P = 0.25$) or minimum average daily movement rates ($F = 1.147$; 1, 13 df; $P = 0.25$) between brooding and non-brooding females during the fall

brooding season. Home range size of both classes of radio-collared females during the fall brooding season varied from 4.2 ha to 21.3 ha. The minimum average daily movement rate ranged from 3.8 to 61.2 m.

Dens were used extensively by both classes of females during the brooding season. Females were located at or near their dens 71.3 $\pm$ 9.8% of the time, and den use did not differ between brooding and non-brooding females ($F = 0.14$; 1, 13 df; $P = 0.71$). The day/night pattern of den use experienced during the summer nesting season continued through the first part of the brooding season (18 Aug - mid-Sept 1988). After mid-September the pattern of den use began to change, and by winter dormancy (1 Nov) females were found away from their dens only during daylight hours.

Home range size of radio-collared females during winter dormancy varied from 0.9 to 15.6 ha. The minimum average daily movement rate ranged from 0.4 to 4.1 m. No broods were seen at den sites or with females during winter. Both females with 1988 broods were sighted with their broods the following spring. No 1987 broods were seen with radio-collared females after the onset of winter dormancy. It could not be determined whether 1987 broods dispersed before or immediately after dormancy. Because of this uncertainty no comparison was made between females denning with broods and those denning without broods.

Females spent more time at or near their den site during winter dormancy than they did during the nesting or brooding seasons ($P <$

0.01). Females were located at their dens 83.1 $\pm$ 6.2% of the time during winter. Fifteen winter readings were made at night and 210 were made during daylight hours.

Home range size of radio-collared females ranged from 4.1 to 109.4 ha during the breeding season and included parts or all of their nesting, brooding, and winter home ranges. Minimum average daily movement rates ranged from 9.7 to 145.2 ha. Females were located at or near their den less frequently during the breeding season than during the other three seasons of the year ($P < 0.01$) (Table 2). Based on successive locations, females appeared to use their dens on a daily basis during the nesting, brooding, and winter seasons. However, as the breeding season progressed, females were frequently located away from their dens as long as 50 hours during 72 hour periods.

Only 2 of the 15 radio-collared females nested in June 1989. The mean home range size of those that nested was 17.6 $\pm$ 6.9 ha versus 29.2 $\pm$ 33.3 ha for those that did not nest. Because of low sample size, statistical comparisons were not possible between females that breed and those that apparently did not breed.

Mean home range size differed among seasons of the year (F = 5.16; 3, 56 df; $P = 0.003$). Female home ranges were larger during the breeding season than during the other 3 seasons of the year ($P <$ 0.05). Minimum average daily movement rates also differed among season (F = 15.50; 3, 56 df; $P = 0.0001$). Movement rates were highest during spring ($P < 0.01$).

The annual home range size of radio-collared females in Lacassine pool varied from 6.1 ha to 165.9 ha (Table 3). Two instances of excessive movement greatly affected mean home range size. When these two females were dropped from analysis, the mean annual home range declined to 25.5 $\pm$ 24.3 ha.

DISCUSSION

Seasonal home range sizes of adult female radio-collared alligators in Lacassine Pool followed the same general pattern as those reported by other authors. Goodwin and Marian (1979) reported that the home ranges of 4 adult females in a north-central Florida lake were largest during spring, intermediate during summer and fall, and smallest during winter. Joanen and McNease (1970) reported the home ranges of 3 adult females, radio-collared in a Louisiana coastal marsh, were larger in spring than in summer and fall. Although alligators followed the same seasonal patterns during the 3 studies mean seasonal home ranges of females in Lacassine Pool tended to be larger. Goodwin and Marion (1979) reported that mean seaosnal ranges varied from 5.7 to 15.6 ha. Joanen and McNease reported mean home ranges of 0.81 - 3.5 ha. The mean home range of adult radio-collared females in Lacassine Pool varied from 4.6 - 27.6 ha.

Although the seasonal home ranges of radio-collared females in Lacassine pool were larger than those reported by Goodwin and Marion (1979) and Joanen and McNease (1970), the mean annual home range size was less than that reported by Taylor (1984) for 9 adult females

monitored in a northern Louisiana lake surrounded by forested wetlands. Taylor reported a mean annual home range of 56.0 ha which was 35% greater than the mean annual home range size of radio-collared alligators in Lacassine Pool. In all studies considerable variation was found among individual alligators. Habitat conditions, prey availability, and sample size could have accounted for differences among studies.

Two instances of excessive movement greatly influenced the mean annual home range size in this study. Shortly after emerging from winter dormancy, one female which had occupied the territory in and around a 14 ha pond, moved to another pond 700 meters away, established a den, and remained in and around the second pond for the remainder of the study. Her home range was estimated by the minimum convex polygon method to be 165.9 ha. However, only 39.7 ha of this area was apparently used. In July 1988 an oil exploration crew established a transect line within 30 m of the den of a second female. The transect line was used extensively as a travel route while blast holes were being drilled for a seismographic survey. After 2 days of disturbance, the female moved 400 m across the marsh to a shallow depression approximately 10 m wide and 100 m long, remained in and around this depression for approximately 3 weeks, then returned to her previously established home range 4 days after the oil exploration crew left the area.

No difference was found among classes of females in either mean home range size or minimum average daily movement rates during the

summer nesting season. This suggests that nesting status and the presence of a previous year's brood do not restrict the activity pattern of adult female alligators. Unquestionably, nest construction and the deposition of eggs would limit a female's activity during the onset of the season. However, nesting females appear to be as active during the remainder of the season as non-nesting females.

Nesting and non-nesting females were found to spend an equal amount of time at or near their dens during the nesting season. This suggests that what has been interpreted as nest attendance by productive female alligators (McIlhenny 1935 and Joanen 1969) may be simply a general tendency for all adult females to use dens heavily during summer daylight hours.

No difference was found in the home range, minimum average daily movement rates, or time spent at or near a den between females with broods and those without broods during fall. This suggests that the presence of a brood neither restricts or enhances a female alligator's activity pattern.

All females used dens as activity centers throughout the year. Thirteen of the fifteen radio-collared changed den sites during the study. Although the timing of these changes generally coincided with a change in reproductive status or biological season, they did not follow a clear pattern. Four of the five females that nested in 1988 changed den sites immediately after the nesting cycle. The remaining nesting female changed den locations the following spring. One

nesting female that occupied a new den after the 1988 nesting cycle relocated to a third site the following spring. Three of the 8 females that did not nest in 1988 or 1989, changed den sites immediately before the onset of winter dormancy and 4 changed den locations shortly after emerging from dormancy. One of the 2 females that nested in 1989 changed den-sites prior to nest construction and 1 maintained the same den location throughout the study. Excluding one female that relocated to a new area in the spring of 1989, the mean distance between successive den locations was 48.6 ± 40.6 m and ranged from 9 to 131 m.

The reason for den relocations could not be determined. The distances involved were apparently too short to provide better access to mates or prey. Likewise the moves did not involve changes in elevation, habitat type, or provide more or less access to open water.

Radio-collared females in Lacassine Pool did not occupy exclusive territories. Ten of the radio-collared females were captured in the same area of the refuge. Considerable overlap in the annual home ranges of alligators within the group occurred. Parts of the annual home ranges of as many as 4 radio-collared females overlapped. The home ranges of several radio-collared females overlapped with non-instrumented females as well. During summer 1988, nests attended by uncollared females were located within the activity ranges of several radio-collared females. Two females, 1

instrumented and 1 non-instrumented, constructed nests and deposited eggs within 30 meters of each other.

Based on radio-collared females, an estimated 29.9% of the adult female alligators in Lacassine Pool nested in 1988. This rate is comparable to those reported in other studies. Taylor (1984) reported an annual nesting rate of 28% based on a telemetric study of 9 adult female alligators monitored in a northern Louisiana lake over a three year period. Wilkinson (1985), working in South Carolina, reported an average annual nesting rate of 25% based radio-collared adult females. Taylor et al. (1987) reported that 25.4% of 370 adult female alligators killed on Marsh Island, Louisiana in 1987 had nested.

Joanen and McNease (1980) reported that 63% of the adult females captured in 1969 on Rockefeller Refuge in Louisiana nested. Sample composition and differences in nutritional conditions could account for the higher nesting rate. Both Wilkinson (1985) and Taylor et al. (1987) found that the probability an adult female would nest increased as the size the female increased. The sample collected by Joanen and McNease (1980) was biased toward larger adult females (Taylor et al. 1987). Also, growth rates and weight-length ratios of female alligators on Rockefeller Refuge were higher than those of females in Lacassine Pool (Chapter 2). This indicates that females in the Rockefeller Refuge sample were in better nutritional condition than those on Lacassine Pool.

Plasma calcium essays indicated that 6 of the radio-collared females in this study were developing ovarian follicles in spring 1988. Of these, 5 eventually laid eggs. Wilkinson (1985) reported similar results; and of 10 radio-collared females with elevated plasma calcium levels in spring, 8 eventually laid eggs. Wilkinson assumed that the difference was the result of stress associated with capture and instrumentation. This may or may not have been the case. Taylor et al. (1987) reported that 19% of 668 adult females alligators examined in summer 1986 and 1987 had developed follicles but did not ovulate or had ovulated and were reabsorbing the resulting ovum. Alligators in both groups would have had elevated plasma calcium levels the preceding spring; however, neither group could have laid eggs. This suggests that plasma calcium assays overestimate the number of females that will eventually nest.

Twelve of the fifteen radio-collared female alligators in Lacassine pool had larger home ranges and higher minimum average daily movement rates during the spring breeding season than they did during any other season of the year. Of these 12, only 2 eventually nested. This suggests that increased activity during spring relates to more than just breeding behavior. Chabreck and Joanen (1979) noted that alligators in southern Louisiana do not feed during winter dormancy and feed at reduced rates during the months of October and March. The resumption of normal feeding activity along with the more moderate temperatures of spring, as compared to the relatively high temperatures of summer and early fall and cool temperatures of

winter, may combine to stimulate alligator activity during the spring season.

The poor nesting rate experience during the second summer the females were monitored may have resulted from improper radio-collar construction. Of the 7 radio-collared females recaptured in September 1989, all appeared to be stressed by the radio-collars. To keep the transmitters positioned on the dorsal surface of the alligators' neck, the collars were manufactured with a metal base plate attached to the inside of the collar band and immediately below the transmitter. Two metal sideplates extended perpendicularly from the baseplate along each side of the alligators' dorsal neck acutes. The sideplates were 1.5 cm long on six of the recovered collars and 3.0 cm long on the seventh. The metal base plate had worn off the bony neck acutes on all seven alligators. The six collars with shorter side plates had rotated so the transmitters were on the ventral side of the alligators' necks. In all six cases, the side plates had cut through the alligator's skin, and into the soft tissue beneath the skin. The one collar with longer sideplates had remained upright but had moved posteriorly into the alligator's pectoral girdle, apparently caused by the animal moving through thick vegetation. The long sideplates appeared to have dislocated both front limbs which had healed in a dislocated position that greatly limiting their mobility.

All seven recovered alligators had grown in total length since the time they were initially captured. Weight-length curves were

generated from alligators captured during a commercial harvest held on Lacassine Pool in 1988 (Chapter 2). The weights of 6 of the 7 recovered alligators were below the expected means for their individual TL. The weights of 2 of these six were outside the 95% confidence limits. The probability by chance alone of 6 of 7 alligators having weights below the expected mean was 0.06. The probability of 2 of the 7 having weights below the 95% confidence limits by chance alone was 0.08. This suggests that the collars did cause a reduction in weight, but the extent to which the stress associated with the radio-collars affected the alligators activity pattern and reproductive processes is unknown. Interestingly, 1 of the 2 alligators that were significantly underweight nested in 1988 and the other nested in 1989.

The type of collars employed in this study are not recommended for future use. A normal collar band with the transmitter located on the ventral side of the alligator's neck should work well if the antennae is constructed so that it extends along the band and above the dorsal surface of the alligator's neck.

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Table 1. Percent of all adult female alligators on Lacassine Pool that nested summer, 1988.

Total length of female (m)	Percent of adult female population[a]	Percent of radio-collared females in size class that nested	Percent of total adult female population that nested[b]
1.83 - 2.13 (6.0 - 6.99 ft)	50.8	25.0	12.7
2.14 - 2.44 (7.0 - 7.99 ft)	44.7	33.3	14.9
> 2.44 (> 8.0 ft)	4.5	50.0	2.3
Total	100.00	N/A	29.9

[a] Determined from 356 adult females harvested from Lacassine Pool, 1983 - 1988.

[b] Column B x column C

Table 2. Seasonal home range size, minimum average daily movement rates, and percent of locations when adult female alligators were < 25 m from their den, Lacassine Pool, June 1988 to June 1989.

Season	Sample size	Number of locations	Home range size (ha)	Minimum average daily movement rates (m)	Percent of locations when females were < 25 m from den
Nesting Season	15	543	13.7±10.2	25.1±17.4	68.6±6.5
(Nesting females)	(5)	(195)	(17.8±16.9)	(27.3±14.1)	(68.8±5.8)
(Non-nesting females without previous year's brood)	(5)	(181)	(10.5±21.2)	(26.7±27.4)	(66.2±6.7)
(Non-nesting females with previous year's brood	(5)	(167)	(12.9±6.1)	(21.2±8.7)	(71.0±7.3)
Brooding season	(15)	327	10.9±4.6	18.6±13.9	71.3±9.8
(Females with broods)	(7)	(156)	(12.5±5.4)	(14.0±8.5)	(70.3±11.7)
(Females without broods)	(8)	(171)	(9.6±3.6)	(22.6±16.9)	(72.3±8.6)
Winter dormancy	15	225	4.6±4.3	1.7±1.1	83.1±6.2

Table 2. (Continued)

Season	Sample size	Number of locations	Home range size (ha)	Minimum average daily movement rates (m)	Percent of locations when females were < 25 m from den
Breeding season	15	350	27.6±30.9	57.9±40.6	56.1±13.8
(Females that nested - June 1989)	(2)	(44)	(17.6±6.9)	(52.1±3.5)	(50.0±19.8)
(Females that did not nest - June 1989)	(13)	(316)	(29.2±33.3)	(58.9±43.8)	(57.1±13.6)

Table 3. Annual home range size of radio-collared adult female alligators, Lacassine Pool, 4 June 1988 to 6 June 1989.

Radio collar number	Total length (m)	Nesting status June 1988[a]	Fall brooding status[b]	Nesting status June 1989[a]	Annual home range (ha)
1553	2.05	NNB	B	NNN	21.8
1884	2.07	NNN	NB	a	27.9
700	2.10	NNN	NB	N	12.9
1614	2.11	N	NB	NNN	45.1
1823	2.14	NNN	NB	NNN	51.8
583	2.19	N	B	NNB	6.1
1801	2.20	N	NB	NNN	10.5
649	2.20	NNB	B	NNN	19.1
610	2.21	NNB	B	NNN	24.6
593	2.30	NNB	B	NNN	165.9

Table 3. (Continued)

Radio collar number	Total length (m)	Nesting status June 1988[a]	Fall brooding status[b]	Nesting status June 1989[a]	Annual home range (ha)
782	2.34	NNN	NB	NNN	14.9
552	2.35	N	B	NNB	96.8
133	2.41	NNB	B	NNN	11.9
185	2.45	NNN	NB	NNN	9.4
204	2.54	N	NB	NNN	17.9
Mean $\pm$ SD	2.25 $\pm$ .15	---	---	---	36.2 $\pm$ 42.6

a/ N = nesting
NNN = non-nesting - no brood present
NNB = non-nesting - previous year's brood present

b/ B = current year's brood present
NB = no current year's brood present

CHAPTER FOUR

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RH: ALLIGATOR SEX RATIOS • Rootes

SEX RATIOS OF AMERICAN ALLIGATORS LIVE-CAPTURED AND HARVESTED BY BAITED HOOKS.

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Abstract: Sex ratios of American alligators (*Alligator mississippiensis*) that were live-captured and harvested by baited hooks from Lacassine National Wildlife Refuge in southwest Louisiana between 1981 and 1988 were compared. Females were more vulnerable to baited hook harvest than live capture (χ^2 = 6.59, 1 df, P = 0.011). Sixty-four percent of 4,631 live-captured alligators, were males; 60% of 1,255 harvested alligators were males. Live-captured alligators were categorized into 3 groups: small juveniles (0.45 - 0.60 m total length [TL]), medium juveniles (0.61 - 1.21 m TL), and large juveniles and adults (> 1.21 m TL). No difference was found in ratio of males to females among the three groups (χ^2 = 1.46, 2 df, P = 0.49). This suggests that alligator sex ratios do not change with age and that smaller alligators (0.45 - 1.21 m TL) provide the same sex ratio estimate as larger animals, which are more time consuming and dangerous to handle.

Key Words: American alligator, Alligator mississippiensis, sex ratio, cloacal examination

Percentages of males and females in American alligator populations have been reported by several authors (Chabreck 1966, Hines et al. 1968, Bara 1972, Palmisano et al. 1973, Wilkerson 1985, and Kinler 1987). All studies were based on alligators that were either live-captured or harvested with baited hooks. The purpose of the study was to compare the sex ratio of live-captured alligators to that of alligators harvested with baited hooks from the same population during approximately the same period of time.

STUDY AREA

The study was conducted on the 12,869-ha Lacassine National Wildlife Refuge in Cameron Parish, southwest Louisiana. A 6,478-ha permanently flooded impoundment located within the refuge served as the principle study site.

The impoundment, referred to as Lacassine Pool consists of floating fresh marsh interspersed with shallow ponds, lakes and canals. Dense, emergent stands of maidencane (Panicum hemitomon), bulltongue (Sagittaria lancifolia), and spikerush (Eleocharis spp.) dominate the marsh. Open water areas range from 0.3 - 1.0 m deep and contain submerged and floating plants including watershield (Brasenia schreberi), fanwort (Cabomba caroliniana), coontail (Ceratophyllum

demersum), American lotus (Nelumbo lutea), and fragrant waterlily (Nymphaea odorata).

METHODS

Each year from 1981 through 1988 approximately 600 alligators ranging in size from 0.35 m to 3.20 m total length (TL) were live-captured by methods described by Chabreck (1963). Most animals were captured during the months of July and August. Sex was determined by cloacal examination (Chabreck 1963) for most animals over 0.45 m. Total length was measured along the animal's dorsal surface. Each animal was marked with 3 like-numbered monel web tags. All data were recorded prior to the animal's release.

An annual commercial harvest was held on the pool in September each year from 1983 through 1988. A total of 1,255 alligators were harvested. Alligators were captured by contract trappers by suspending baited hooks approximately 0.2 m above the water's surface (Palmisano et al 1973). Prior to removal from the area the total length of each harvested alligator was measured along its dorsal surface and its sex was determined by cloacal examination (Chabreck 1963). Legal restrictions limited the harvest to alligators > 1.21 m TL. Chi-square test of homogeneity was used to test sex ratios among alligator size categories and between capture methods (Steel and Torrie 1980).

RESULTS AND DISCUSSION

Live-captured alligators were grouped into 3 categories: small juveniles (0.45 - 0.61 m TL), medium size juveniles (0.61 - 1.21 m TL) and large juveniles and adults (> 1.21 m TL) (Table 1). Only large juveniles and adults were harvested by baited hooks. Percent male alligators did not differ among the three groups of live-captured alligators ($\underline{x}^2$ = 1.46, 2 df, P = 0.49). The three categories were pooled and compared to harvested alligators and the percent males differed between the two groups ($\underline{x}^2$ = 6.59, 1 df, P = 0.011). Females were slightly more vulnerable to September baited hook harvest than to summer live capture. Of 4,631 live-captured alligators, 63.7% were males while 59.8% of the 1,255 harvested alligators were males.

Most live-captured alligators were caught in marsh or shallow lake habitat. Alligators in deeper canals were less tolerant of human approach and frequently dove out of reach of captors. A majority of the harvested alligators were taken from canal and deeper lake habitat. Open waterways provided easier transportation routes for trappers than the denser marsh vegetation. It is unlikely these differences in capture sites had an effect on the observed sex ratios. Hines, et. al (1968) and Joanen and McNease (1970 and 1972) hypothesized that male alligators tended to dominate canal habitat and females were more abundant in the marsh. This would indicate the harvested group should have the highest percentage of males, the opposite of what was observed. No difference (P = 0.74) was found in

the sex ratios of alligators harvested from canal, marsh and lake habitat in Lacassine Pool during the 1988 trapping season (Chapter 2).

Although a statistical difference was found in the sex ratio of alligators captured by the two methods, the large sample sizes involved allowed even small differences to be detected. From a practical standpoint, the differences found in this study were not biologically meaningful.

Based on growth curves developed from alligators on Lacassine Pool (Chapter 2) the mean age of alligators in the small juvenile category was 16 months; the mean age of medium size juveniles were 40 months; and all alligators in the large juvenile and adult category would be expected to be older than 60 months. No difference in the sex ratio of live-captured alligators was found among these three categories. This suggests that the sex ratio in alligators does not change with age, at least once a 0.45 m TL is reached.

Joanen and McNease (1978) reported alligator < 0.61 m TL could not be sexed accurately by cloacal examination. Their observation was based on a sample size of 28. In this study no difference was found between the sex ratio of 0.45 - 0.60 m TL live-captured alligators and that of larger live-captured animals. Apparently, if errors in sex determination were made they were non-directional in nature. Recapture data tends to support this conclusion. Seventy-nine small juveniles were recaptured after growing into larger size classes. Two alligators that were initially classified as males were

subsequently reclassified as females and 2 that were originally classified as females were reclassified as males. This indicates a non-directional error rate of about 5%.

Although a statistical difference was found, from a management perspective, live capture methods (Chabreck 1963) and harvest by baited hooks (Palmisano et al. 1973) provided comparable estimates of the populations sex ratio. Further, small alligators (0.45 - 1.21 m TL) which are relatively easy to live capture in large numbers, provided the same sex-ratio estimated as larger animals which are more time consuming and dangerous to handle.

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Table 1. A comparison of sex ratios of alligators live-captured and harvested by baited hook from Lacassine Pool, 1981-1988.

	Small juveniles (0.45 - 0.60 m TL)			Medium juveniles (0.61 - 1.21 m TL)			Large juveniles & adults (> 1.21 m TL)		
Capture method	Number males	Number females	Percent males	Number males	Number females	Percent males	Number males	Number females	Percent males
Live captured	1,420	836	62.9%	1,227	668	64.7%	304	176	63.3%
Harvested by baited hook		N/A			N/A		750	505	59.8%

CHAPTER FIVE

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RH: ALLIGATOR HABITAT · Rootes

COMPOSITION OF ALLIGATOR POPULATIONS IN RELATION TO HABITAT TYPES.

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Abstract: Sex ratios, mean total lengths, and adult/large juvenile ratios (1.21-1.82 m total length) of American alligators (*Alligator mississippiensis*) harvested by baited hooks from marsh (< 40% open water), lake (> 60% open water), and canal habitats on Lacassine National Wildlife Refuge in 1988 were compared. The mean total length of alligator harvested from lakes was less than that of alligators harvested from canals and the marsh. The difference was mainly related to the distribution of large juveniles (1.21 - 2.12 m TL alligators). Proportionately more large juveniles were harvested from lakes (X^2 = 5.20, 1 df, P = 0.02). The sex ratio of alligators did not differ among habitat types (X^2 = 0.062, 2 df, P = 0.74).

Key Words: American alligator, *Alligator mississippiensis*, sex ratio, habitat

Various studies have documented alligator habitat preferences (Chabreck 1965, Hines et al. 1968, Joanen and McNease 1970 and 1972,

McNease and Joanen 1974, and Goodwin and Marion 1979). Estimates of habitat use by adult alligators has generally been based on casual observation (Hines et al. 1968) or on radio-collared alligators (Goodwin and Marion 1979 and Joanen and McNease 1970 and 1972) that were captured and released in what may have been a previously established activity range. The purpose of this study was to compare the sex ratios and size classes of alligators harvested by baited hooks (Palmisano et al. 1973) from marsh, lake, and canal habitats on Lacassine National Wildlife Refuge in southwest Louisiana.

STUDY AREA

The study was conducted on the 12,869-ha Lacassine National Wildlife Refuge in Cameron Parish, southwestern Louisiana. A 6,478-ha permanently flooded impoundment located within the refuge served as the principle study site.

The impoundment, referred to as Lacassine Pool, consists of floating fresh marsh interspersed with shallow lakes, ponds, and canals. Dense, emergent stands of maidencane (*Panicum hemietomon*), bulltongue (*Sagittaria lancifolia*), and spikerush (*Eleocharis* spp.) dominate the marsh. Open water areas range from 0.3 - 1.0 m deep and contain submerged and floating plants including watershield (*Brasenia schreberi*), fanwort (*Cabomba caroliniana*), coontail (*Ceratophyllum demerum*), American lotus (*Nelumbo lutea*), and fragrant waterlily (*Nymphaea odorata*).

METHODS

In September 1988 a commercial alligator harvest was held on Lacassine Pool. Alligators were captured by contract trappers by suspending baited hooks 0.2 - 0.3 m above the water's surface. Beef lungs were used as bait. On selected days observers accompanied trappers on their morning rounds. A total of 622 baited hook sets were inspected. These sets produced 124 alligators. As alligators were removed from the sets they were marked with a numbered harvest tag. Observers classified the habitat at each capture site into one of three categories, marsh (< 40% open water), lakes (> 60% open water) or canals. Prior to removal from the refuge, the total length (TL) of each alligator was measured along its dorsal surface and its sex was determined by cloacal examination (Chabreck 1963).

Legal restrictions limited the harvest to alligators > 1.20 m TL. Palmisano et al. (1973) reported the baited hook harvest method was biased toward adult alligators (> 1.82 m TL). Since identical capture methods were used in all habitats, the probability of catching a large juvenile (1.21 - 1.82 m TL), although biased, would be the same for each habitat type. This should allow for valid comparisons by size and sex classes among habitats.

ANOVA was used to test for differences in the total length (TL) of alligators captured from different habitats. When differences were found Duncans multiple range test was used to separate means. Chi square test of homogeneity was used to test sex and adult/large juvenile ratios among habitats (Steel and Torrie 1980).

RESULTS AND DISCUSSION

Mean total length of alligators taken differed among habitats ($F = 3.31$; 2, 118 df; $P = 0.04$) with larger alligators being taken from marsh and canal habitats ($P < 0.05$). Mean length of alligators taken from lakes was 2.07 $\pm$ 0.42 m versus 2.28 $\pm$ 0.47 m for alligators taken from canals and the marsh. This difference was mainly attributable to distribution of large juveniles (Table 1), more of which were harvested from the lakes than from canals and the marsh ($X^2 = 5.20$, 1 df, $P = 0.02$). When large juveniles were dropped from analysis, the mean TL of adults did not differ among habitats ($F = 0.71$; 2, 93 df; $P = 0.49$).

The concentration of large juveniles in lake habitat is consistent with other reports (Giles and Childs 1949, Chabreck 1965, and McNease and Joanen 1974). This may be related to prey availability. Large juveniles in South Louisiana have been shown to prey extensively on crustaceans (Giles and Childs 1949 and Chabreck 1971). This prey type may be more available to the alligators in shallow lakes than in marsh and canal habitats. Also, lakes contained dense stands of floating leaved and emergent aquatic plants such as watershield, fragrant waterlily, and American lotus which offer cover to large juveniles. Selection by smaller animals of habitat that offers concealment and escape from larger animals may provide a means of avoiding cannabilism (Rootes 1989).

The sex ratio (Table 1) of combined sizes of alligators ($X^2 = 0.62$, 2 df, $P = 0.74$) and adult alligators ($X^2 = 0.59$, 2 df, $P =$

0.76) did not differ among habitat types. This contradicts reports by other authors. Hines et al. (1968) and Joanen and McNease (1970 and 1972) concluded male alligators dominate canals and females are more heavily represented in marsh habitats. Even if the sex ratio estimates in this study (Table 1) represented true differences they are not of a magnitude to support these conclusions. This is further confirmed by the distribution of large bulls (> 2.75 m TL), which were equally represented in marsh and canal habitats ($\underline{x}^2$ = 0.25, 1 df, P = 0.77). Seven bulls > 2.75 m TL were harvested from both canals and the marsh. They composed 22% of the harvest from canals and 18% of the marsh harvest. This suggests that the distribution of male and female radio-collared alligators (Joanen and McNease 1970 and 1972) may have been a function of where the animals were captured and their traditional territory. Fourteen of fifteen radio-collared adult females monitored on Lacassine Pool between June 1988 and June 1989 (Rootes 1989) spent nearly all of their time in marsh habitat. However, all 14 were captured and released in marsh habitat. The one female that spent considerable time in lake habitat was captured and released in lake habitat.

The distribution patterns of large juveniles and adult males and females may extend beyond the fall harvest season. Females in Lacassine pool frequently constructed nests along canals in June 1987 and 1988. Likewise large juveniles appeared to be concentrated in lake habitat, and large bulls were frequently observed in marsh

habitat during alligator tagging projects held in April, July, and August 1987 and 1988 on the pool.

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Table 1. Comparison of total length (m), sex ratios, and adult-large juvenile ratios of alligators harvested from canal, marsh and lake habitats in Lacassine Pool, 1988.

	Habitat Types		
Parameter	Canal	Marsh	Lakes
Total Length (m) (Mean ± SD)			
Combined Sexes	2.24 ± 0.53 (n=32)	2.31 ± 0.47 (n=40)	2.07 ± 0.42 (n=52)
Males	2.44 ± 0.55 (n=20)	2.45 ± 0.57 (n=23)	2.13 ± 0.46 (n=28)
Females	1.93 ± 0.28 (n=12)	2.13 ± 0.14 (n=17)	2.00 ± 0.36 (n=24)
Ratio males:females			
Combined Sizes	62:38 (n=32)	57:43 (n=40)	54:46 (n=52)
Adults	62:38 (n=26)	58:42 (n=36)	53:47 (n=36)
Ratio adults:juveniles	81:19 (n=32)	90:10 (n=40)	69:31 (n=52)

APPENDIX

Table 1. Comparison of the TL of predator alligators with the TL of their cannibalized prey, Lacassine Pool, 1987 and 1988.

Predator harvest tag number	Predator TL (m)	Prey web tag number	Prey estimated TL (m) at time cannibalized
5248	1.55	202	0.28
5549	2.34	1332	1.62
5295	2.03	3123	0.61
5295	2.03	3120	0.54
5586	1.47	3132	0.54
5409	3.00	3210	1.05
5409	3.00	2376	1.35
5481	3.05	1297	1.61
5581	2.82	2488	1.31
5561	2.82	4057	2.15
5546	3.15	1329	1.89
5488	3.20	1550	1.79
5395	3.36	908	1.79
5395	3.36	1476	1.76
5339	3.05	2568	1.33
5339	3.05	1291	1.77
5476	2.39	1375	1.44
5476	2.39	1294	1.59
5662	2.49	2682	1.33
5526	1.86	3523	0.56
5374	1.45	3396	0.59
3791	1.84	4335	0.59
3791	1.84	5134	0.49
3799	2.09	3597	0.44
3800	1.61	4334	0.64
4046	2.05	5437	0.36
4046	2.05	5083	0.49
5171	2.05	5171	0.27
3826	1.79	5205	0.27
3835	1.84	5291	0.53
4059	1.51	5065	0.49
3914	1.72	5059	0.59
3942	1.67	5191	0.31
3976	1.49	5324	0.62
4175	2.12	4588	0.84
4175	2.12	5352	0.51
3849	2.92	1112	1.97
4161	2.18	2300	0.92
4162	3.18	2978	1.10
4266	2.15	5345	0.41

Table 1. (Continued)

Predator harvest tag number	Predator TL (m)	Prey web tag number	Prey estimated TL (m) at time cannibalized
4278	2.17	3550	0.74
3786	2.06	4540	0.97
3786	2.06	5107	0.54
3842	1.92	3179	0.72
3842	1.92	3168	0.72
3842	1.92	4351	0.79
3847	3.00	2805	1.23
3860	1.56	5170	0.26
3860	1.56	5217	0.26
4036	2.28	4544	0.72
3794	3.26	1796	1.64
3852	2.87	4268	2.10
3852	2.87	3841	1.67
3852	2.87	5053	0.59
3884	3.69	928	1.78
3950	2.15	3542	0.79
4172	2.47	2663	1.00
4173	2.69	3300	0.85
4149	2.97	10	1.56
4066	2.55	4645	0.82
4066	2.55	4647	0.72
4178	2.97	2771	1.41
4140	2.97	1917	1.51
4140	2.97	2296	1.15
3936	3.27	3006	1.41
4145	2.79	2978	1.15
3912	3.29	1900	1.82
3927	3.14	443	2.00
4216	3.08	2828	1.36
4171	3.02	4460	0.63
3921	3.05	5559	0.69
3921	3.05	4638	1.03

Table 2. Cannibalism of marked alligators age 11 months and older identified from stomach contents of alligators taken from Lacassine Pool.

Predator TL (m)	Number of stomachs examined	Cases of cannibalism identified	Cases per 100 stomachs examined
Males			
1.22-1.51	42	2	4.8
1.52-1.82	78	5	6.4
1.83-2.12	97	8	8.2
2.13-2.42	46	5	10.9
2.43-2.73	47	6	12.8
2.74-3.04	50	18	36.0
> 3.04	46	14	30.4
Total Males	406	57	14.0
Females			
1.22-1.51	33	2	9.1
1.52-1.82	67	5	7.5
1.83-2.12	93	7	7.5
2.13-2.42	99	7	7.1
2.43-2.73	8	--	--
Total Females	300	21	7.0

APPENDIX · Rootes

VITA

William L. Rootes was born on March 16, 1949 in Jefferson City, Missouri to Mr. and Mrs. William A. Rootes. He graduated from Jefferson City Senior High School in 1967. He received a Bachelor of Arts degree in Business Administration from Central Methodist College, Fayette, Missouri in 1971. He attended Graduate School at University of Missouri, Columbia and received a Master's of Public Administration degree in 1986. He entered graduate school at Louisiana State University in August 1986 and is currently a candidate for the degree of Doctor of Philosophy in Wildlife and Fisheries Science.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: William L. Rootes

Major Field: Wildlife and Fisheries Science

Title of Dissertation: Behavior of the American Alligator in a Louisiana Freshwater Marsh

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

December 1, 1989