BEHAVIORAL ECOLOGY OF YOUNG AMERICAN ALLIGATORS

By

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The behavior and ecology of young *Alligator mississippiensis* were studied at several north and central Florida localities. Growth and movement rates were calculated from recaptures of tagged alligators. Growth rates varied significantly with habitat, and were intermediate between rates reported for south Florida and South Carolina alligators. There were no significant differences between growth of male and female juveniles.

Survivorship of alligators through their first post-hatching year was .30 for juveniles from lake habitats and .17 for shallow marsh juveniles. Two-year survivorship was .14 for a small sample of lake animals. Injuries were significantly more frequent in shallow marsh than in lake juveniles, suggesting that increased predation on alligators in marsh habitats was responsible for the higher mortalities there.

Pods (sibling groups of hatchling alligators) remained near the nest for a mean of 14 days after hatching. Most pods at this time were found in the guard pools created and used by the adult female alligator during incubation. Movement of pods from the nest to the mother's den

where they overwintered included stops at small pools which were apparently created by the parent. Pod dispersal began in June of the year following hatching, but after one year most juveniles were still within 200 m of the den. One to two-year old alligators continued to disperse, and it appeared that most two-year-olds had lost all contact with their natal areas. Rates of movement of juveniles greater than 31 cm snout-vent length also varied with locality, and were identical for males and females.

Hatchling alligators emerged synchronously to bask each morning about one hour after sunrise. Emergence was accompanied by a marked increase in vocalization, and resulted in an extremely close aggregation of all pod members (social bask). After the morning bask hatchlings spent the remainder of the day in the water, largely inactive. At sunset, pods again began to vocalize rapidly as individuals emerged from cover and dispersed to forage. Average rates of vocalization for the first hour after sunset were significantly higher than rates observed during the day. Shortly before sunrise most individuals returned to the vicinity of their initial emergence point; final reaggregation of pods took place during the social bask.

Juveniles emitted the juvenile grunt vocalization in most contexts involving movement by juveniles or by the parent. Grunts were used as homing signals by juveniles when separated from the pod. The high-intensity grunt, or juvenile distress call, emitted in distress contexts was not clearly distinct from grunts used in other contexts.

Parental care involving regular maternal attendance or defense was observed for 34% of all pods. Duration of care was variable: one pod was defended through June. A history of human disturbance at some

localities was associated with low observed frequencies of pod attendance and defense. Adult females threatened intruders with a series of threat displays also employed in other intra- and interspecific agonistic encounters. Vocalizations of juveniles were important in provoking defensive behavior by adults.

Playbacks of recorded juvenile grunts attracted adult and subadult alligators of both sexes. Adult females responded to playbacks more rapidly and employed the inflated posture more often than adult males. Hatchlings presented to two females during playbacks were taken into the mouth and released unharmed. Juvenile alligators in the field were initially attracted to playbacks of juvenile grunts, but sought cover if playbacks were continued. In artificial enclosures, juveniles were consistently attracted to such playbacks. These experiments suggested that the juvenile grunt functions to alert other juveniles and adults to novel stimuli without conveying any information on their nature.

CHAPTER I INTRODUCTION

Few extant reptiles command the awe that has been accorded to crocodilians. Human fascination with crocodilians is long-standing; crocodilians are prominent in the mythology of many tropical cultures. As others have noted, the writings of many early New World naturalists reflect little reluctance to borrowing from this mythology when describing crocodilian life histories. While this has made for some fascinating reading, it has left the credibility of many authors to question. Contradictory descriptions of the behavior and ecology of many species of crocodilians abound, and it has become common for crocodilian natural history accounts to begin with a discussion of how crocodiles do not behave (e.g., McIlhenny, 1935; Neill, 1971). Scientific evidence sufficient to resolve some of these controversies has accumulated only within the last fifteen years. Many workers familiar with the behavior of other reptiles have found early descriptions of courtship display or parental care in crocodilians impossible to accept (e.g., LeBuff, 1957). Some of this skepticism is understandable in light of the other incredible tales associated with crocodilians. Certainly Pooley's (1977) photographs and accounts of parental care in *Crocodylus niloticus* are no less remarkable than Topsell's discourse on the Crocodile of the Nilus in 1608.

The confusion regarding many published accounts of crocodilian natural history is augmented by the behavior of the subjects themselves.

Crocodylians are nocturnal, and even by day secretive and difficult to observe. Many species occupy densely vegetated or remote areas. In addition, they are behaviorally very sophisticated reptiles. Recent work has demonstrated that crocodylians possess well-developed sensory abilities (Bellairs, 1971), display repertoires and social systems (Modha, 1967; Garrick and Lang, 1977; Garrick *et al.*, 1978), learning abilities (Northcutt and Heath, 1971) and reproductive behaviors which include extensive parental care (Hunt, 1975; Pooley, 1977).

Most of the generalities about crocodylians can be applied to the American alligator, *Alligator mississippiensis*. Neill (1971) has reviewed much of the 18th and 19th century alligator lore, and discusses the practice of applying Old World crocodile fables to American alligators. Neill decries those writers whom he believes to have been most guilty of legend-mongering or an unscientific approach. Unfortunately, Neill himself falls into this category at times, and his book inadvertently serves as an example of the phenomenon it seeks to end (see reviews of Neill, 1971, by Fogarty, 1972, and King, 1972).

More accurate life histories (in general) of the American alligator were provided by Reese (1915) and McIlhenny (1935). Both of these were largely narrative and the data presented were of limited value.

Renewed conservation interest in the alligator beginning in the 1960's has led to some preliminary quantitative studies on growth (Hines *et al.*, 1968), feeding (Fogarty and Albury, 1967; Chabreck, 1971; Valentine *et al.*, 1972), movements (Chabreck, 1965; Joanen and McNease, 1970, 1972a; McNease and Joanen, 1974) and population dynamics (Chabreck, 1966; Joanen and McNease, 1972b). The severely declining

status of many alligator populations at this time has also made new information on reproductive ecology and behavior vitally important; in this area especially the speculations and anecdotes of earlier workers have been supplemented with more extensive data from recent field studies.

The reproductive cycle of *Alligator mississippiensis* begins in March, when an increase in bellowing and courtship display by adult males and females is observed (Joanen and McNease, 1975; Garrick *et al.*, 1978). Increased movements by adults of both sexes, presumably related to mating activities, are also observed from March through late May (Joanen and McNease, 1970, 1972a; Goodwin, 1977). Most actual mating in the wild in Florida probably occurs in May (Garrick *et al.*, 1978; pers. observations). Nest construction in north Florida normally begins in mid-June, possibly depending on air or water temperatures; the amount of time spent in nest construction may be somewhat longer in Florida than in Louisiana, but eggs are apparently laid at about the same time (Joanen, 1969; Deitz and Hines, in press).

There has probably been more controversy surrounding the subsequent reproductive behaviors and parental care by female *Alligator mississippiensis* than any other aspect of alligator natural history; the confusion in the literature is certainly long-standing. William Bartram's description of alligator habits in 1791 includes the statement: "...certain it is, that the young are not left to shift for themselves; for I have had frequent opportunities of seeing the female alligator leading about the shores her train of young ones, just as a hen does her brood of chickens; and she is equally assiduous

and courageous in defending the young... ." (Bartram, 1791, p. 122).

Unfortunately, many of Bartram's other statements about alligators are exaggerated or erroneous. Parental care after hatching was also referred to by Audubon in 1827 and by some of his contemporaries (see Neill, 1971). But beyond these narratives, few scientific investigations of alligators have reported any after-hatching care. Reese (1915) stated that the female alligator liberated the young from the nest in response to their vocalizations, but did not discuss their fate after this. Kellogg's (1929) review concludes that it is "generally accepted that the adults do not show any special consideration for the young after they are hatched," but also allows (with reference to Bartram) that "such may not always be the case" (Kellogg, 1929, p. 13).

McIlhenny's (1935) book on alligator natural history described parental behaviors previously unreported for any crocodilian, or in fact any reptile. Alligator nest-guarding and nest opening behaviors were discussed, and McIlhenny became the first to describe: 1) the movement of young from the nest to the den site, led by the female; 2) the persistence of the aggregation of young alligators, hereafter referred to as a pod, into the following spring; 3) defense of the pod by the female through the following spring; 4) growth and food habits of young alligators; and 5) the eventual dispersal and maturation of juveniles. As Carr (1976) pointed out, most of McIlhenny's observations were subsequently proven accurate. His account was, like its predecessors, primarily narrative, and until recently there were few quantitative data available on alligator behavior.

Chabreck (1965) provided additional reports of the movement of young alligators from nest to den, and followed McIlhenny in implying

that there was a limited amount of protection by the parent. Both Chabreck (1965) and McIlhenny (1935) worked with Louisiana coastal marsh alligators, and indicated that in this habitat pod dispersal began in spring. Fogarty (1974) reported that young alligators in the Florida Everglades may remain near the female's den for two or three years after hatching, but denied the existence of any active protection by the parent. Several large scale studies of alligator nesting ecology, covering most of the animal's present range, were recently completed; all of these reported a variable degree of nest attendance by the female and in most instances opening of the nest by her in order to liberate the young (Joanen, 1969; Fogarty, 1974; Metzen, 1977; Deitz and Hines, in press). Of all the accounts since McIlhenny only one, based on a single observation, provided any further direct evidence for parental care of the young after hatching (Kushlan, 1973).

At the inception of this study most other aspects of juvenile alligator behavior and ecology remained equally obscure. Despite the wide variety of wetlands habitats occupied by alligators, information on growth and movements was available only for the Louisiana coastal marshes and, to some extent, for the Everglades; no data were available on the influence of habitat on life history parameters. Observations suggesting that the vocalizations of young alligators were the principle mechanism by which pod cohesion was maintained were made by Campbell (1973) and Herzog (1974), but no experiments had been performed to test this hypothesis.

The variety of habitats occupied by *Alligator mississippiensis* in north and central Florida provided an opportunity to examine juvenile behavior in different ecological contexts. I began this

investigation to: 1) obtain information on the growth, mortality, movements and dispersal of juvenile alligators in Florida; 2) determine the extent and persistence of parental care; 3) examine communication and social behavior within the pod through field observations and experiments; and 4) determine the influence of habitat on the above by studying juveniles in different locales. Several excellent accounts of social behavior and parental care in other species of crocodilians appeared during the study (*e.g.*, Garrick and Lang, 1977; Pooley, 1977). Consequently, it also became possible to make some preliminary comparisons between *Alligator mississippiensis* and other crocodilians with respect to the ecological and evolutionary significance of parental care and juvenile social groups.

CHAPTER II STUDY AREAS

Orange and Lochloosa Lakes

Orange and Lochloosa Lakes (Alachua County) form a twin-lake system connected by Cross Creek, which runs from southwest Lochloosa Lake to northeast Orange Lake (Fig. 2-1). Both are large mesotrophic lakes, with extensive marshy areas covering portions of the basin (Brezonik and Shannon, 1971; Table 2-1). Most observations of juveniles were in these marshy areas, although several groups of juveniles were located along the marshy fringe around the open water portions of the lakes. Characteristic of marsh areas of these lakes is a heavy build-up of peat. Gasses formed by decomposition bring large chunks of peat to the surface, resulting in floating islands and floating mats extending out from the lake shore. Vegetational composition of these islands and fringe areas is largely *Sagittaria lancifolia*, *Cladium jamaicensis*, *Hydrocotyle umbellata*, *Panicum* sp., *Myrica cerifera*, *Cephalanthus occidentalis* and *Decodon verticillatus*. *Nuphar luteum* covers extensive portions of the open water margins, with *Eichornia crassipes*, *Limnobium spongia* and *Pistia stratiotes* common in more sheltered areas. There is abundant submerged growth of *Hydrilla verticillata*.

Seasonal variation in water temperature at Orange Lake is shown in Fig. 2-2. Predictably, shallow water areas in the lake fringe and marsh regions showed greater diel fluctuation, heating up rapidly in

Table 2-1. Study areas.

Location	Mean Depth (m) ¹	Surface Area (ha) ²	Trophic State Index ¹
1. Orange Lake	1.8	5330	4.3 - Mesotrophic
2. Lochloosa Lake	2.9		5.2 - Mesotrophic
3. Lake Griffin	2.4	4310	13.7 - Hypereutrophic
4. Station Pond	< 1	242	(3.6 - Mesotrophic)
5. Payne's Prairie	0.4 - 0.9	5036	---
6. Lake Wauberg	3.8	101	7.4 - Eutrophic
7. Biven's Arm	1.5	58	14.7 - Hypereutrophic
8. Carr property	> 1	ca 5	---

¹ Values for mean depth and trophic state index are from Brezonk and Shannon (1971) except values from Payne's Prairie which are from White (1974).

² Surface areas taken from U.S. Geological Survey data, or calculated from aerial photographs via planimetry.

Figure 2-1. Locations of principal study areas in north and central Florida. Numbers correspond to Table 2-1. Dashed portions of areas 1 and 2 indicate the marsh areas of Orange and Lochloosa Lakes.

Figure 2-2. Seasonal changes in water temperatures of Orange Lake, Lake Griffin and Payne's Prairie.

the sun and cooling below average lake temperature at night. Water levels fell gradually throughout the study period until 1977, when abnormally low rainfall resulted in a 20-year low in the lake level (Fig. 2-3b). This produced exposed mudbanks around lake shores and an extension of the fringe vegetation into the center of the lake. The Orange Lake alligator population at the height of the drought was estimated at over 2500 individuals based on night census data (Hines, unpub. data).

Payne's Prairie

Payne's Prairie (Alachua County) is a large solution prairie typical of Florida wet prairie habitat, except that drainage canals and levees have been constructed throughout for flood control. It is now a portion of Payne's Prairie State Preserve. White (1974) has presented data on hydrology, vegetation and dynamics of plant succession on Payne's Prairie. Alligators are commonly found only in the wetter portions of the basin. Dominant plant species in these areas include *Pontederia cordata*, *Jussiaea peruviana*, *Typha* sp., *Salix carolinensis*, *Panicum hematonon*, *Juncus effusus*, *Nelumbo lutea* and *Hydrocotyle umbellata* (White, 1974). Water levels during the study period are presented in Fig. 2-3a; drainage of Payne's Prairie has been artificially controlled since mid-1976. Water temperatures show daily fluctuations, in keeping with the shallow depth throughout most of the marsh. Seasonal temperature changes are presented in Fig. 2-2.

Aerial nest surveys in 1976-1977 and casual observations at night indicated that Payne's Prairie probably supports an alligator population comparable to Orange Lake in density, but no censuses were conducted.

Figure 2-3. Water levels at three study sites, 1975-1977: Payne's Prairie, top; Orange Lake and Lake Griffin, bottom.

Lake Griffin

Lake Griffin (Lake County) is the last lake in the Oklawaha Basin chain of lakes; it drains directly into the Oklawaha River. All observations in this study were conducted in Picciola Cove, in the southwestern portion of the lake. As in Orange Lake, peat build-up has produced a floating mat around the fringe of the lake; in Lake Griffin this forms a dense thicket rather than a floating marsh, composed principally of woody plants such as *Acer rubrum*, *Cephalanthus occidentalis*, *Salix carolinensis*, and *Nyssa sylvatica*. There are emergent growths of *Sagittaria* sp., *Nuphar luteum* and *Panicum repens*. Alligators of all sizes used trails and holes in this fringe.

Lake Griffin was characterized by Brezonik and Shannon (1971) as hypereutrophic (Table 2-1). The development of this condition was due in part to high volumes of citrus cannery and municipal sewage effluent, and also to artificial stabilization of water levels. Water level fluctuations were minimal during the study (Fig. 2-3b). Water temperatures (Fig. 2-2) averaged higher than in Orange Lake, probably as a result of its more southerly location and greater depth (Fig. 2-1; Table 2-1).

Alligator reproduction on Lake Griffin has been explosive in recent years. This has produced populations which are extremely dense and composed largely of juveniles less than 150 cm in total length (Hines unpub. data; pers. observations).

Station Pond

Station Pond (Levy County) is the only study area located in the Gulf Coast drainage (Fig. 2-1); it forms part of the headwaters of the Waccasassa River. It is a shallow, sand-bottomed basin, surrounded mostly by pine flatwoods except at the southwestern end where it grades into cypress swamp. Principal emergent plant species in the marsh were *Panicum hematomon*, *Nymphaea odorata*, *Brasenia schreberi*, and *Pontederia cordata*. Slightly higher islands in the marsh, referred to as "heads," were often associated with alligator holes. Vegetation on these heads was predominantly *Panicum hematomon*, *Cephalanthus occidentalis*, *Sagittaria lancifolia*, and a variety of undetermined species of ferns and herbs; some heads also included one or two cypress trees, *Taxodium distichum*.

No monthly water level or temperature data are available for Station Pond; temperature data available for Payne's Prairie (Fig. 2-2) are probably a reasonable approximation. The water level of Station Pond appears dependent on regular rainfall, for during periods of low rainfall it would drop markedly. Station Pond became completely dry in May 1977, and except for a brief reflooding after rains in September, remained dry until January 1978. During this drought, the only surface water available was in alligator holes--depressions which are deepened and kept clear of emergent vegetation by the activity of the resident alligator (see McIlhenny, 1935, and Craighead, 1968). Prior to 1977 the alligator population on Station Pond was estimated at 90-120 individuals (Hines, Woodward and Deitz, unpub. data).

Brazonik and Shannon (1971) have presented productivity and water chemistry data for Watermelon Pond, a marsh which is slightly deeper but otherwise very similar in appearance to Station Pond. Watermelon Pond is also in the Waccasassa drainage and is located 2.2 km to the northeast of Station Pond. The trophic state index for Watermelon Pond has been used for Station Pond (Table 2-1).

Occasional data were also obtained on alligators in three other locations, all in Alachua County: Biven's Arm and Lake Wauberg, both part of the Payne's Prairie drainage system, and a small pond on the property of A. F. Carr, Jr., near Micanopy, Florida (Fig. 2-1). Significant features of these study areas are discussed with results as appropriate.

CHAPTER III GROWTH, MORTALITY AND MOVEMENTS OF JUVENILE ALLIGATORS

Introduction

Quantitative ecological studies of crocodilians have been few, and with the exception of Cott's (1961) work with *Crocodylus niloticus* have been restricted to populations occupying single habitat types. Most data on growth and mortality in *Alligator mississippiensis* have come from the Louisiana coastal marshes, where salinity is the only major environmental variable affecting populations in different marsh areas (Joanen and McNease, 1972b; Chabreck, 1965, 1971). Growth rates of Louisiana and south Florida juvenile alligators are comparable (McIlhenny, 1935; Hines *et al.*, 1968) and are both much higher than rates reported for South Carolina (Bara, 1972; Murphy, 1976), suggesting that length of the active season is important. Data on natural mortality of *A. mississippiensis* (or of most other species) are non-existent, except for indirect conclusions based on life tables (Nichols *et al.*, 1976).

Chabreck (1965) described the post-hatching movements of *A. mississippiensis* in Louisiana, and indicated that they were influenced by water levels. Similar results were reported from the Everglades (Fogarty, 1974), and formation of pods was apparently typical after hatching in both areas. The duration of these pods, distance moved and extent of interaction with the parent were not clearly defined. Neill's (1971) assertions that Florida juveniles did not form groups were entirely unfounded, but the extent to which lake habitats in north

and central Florida might cause divergence from marsh movement patterns was unknown. The implications of Chabreck (1965) and Fogarty (1974) that pod formation, dispersal and possibly duration of parental care were affected by water levels and other habitat characteristics indicated that information on the natural history of Florida juvenile alligators was basic to any understanding of the significance of social behavior and parental care.

Methods

Alligator nests were located on Orange and Lochloosa Lakes and Station Pond using aircraft, and on Payne's Prairie by searching levees on foot. Brushy cover in the fringe areas of Lake Griffin made both air and ground searches for nests there impractical, and only two were located. Nests were usually checked semi-weekly and observations on female behavior were made at this time. Observations of one nesting female were also made at the Carr property. After hatching, pods were followed on foot or by canoe on Payne's Prairie and at Carr's, and by boat on Orange Lake and Lake Griffin.

Most alligators were captured at night--those under 155 cm in total length by hand or with tongs. Snout-vent length (SVL, taken from the tip of the snout to the posterior angle of the vent), total length (TL), and weight were normally recorded for all alligators captured. Evidence of injuries was also recorded. Loss of the tail tip, *i.e.*, the distal 20% of the tail, was considered to be a minimal disfigurement; loss of a limb or a substantial portion of the tail and significant

scars or wounds on the head or trunk were considered to be severe injuries. Sex was determined by cloacal examination for specimens with a TL of 45 cm or greater (Chabreck, 1963). Locations of all captures and recaptures were plotted to the nearest 100 m using aerial photographs; even more precise locations were usually possible with this method. Alligators were marked with monel tags (National Band and Tag Co., Newport, Ky.) inserted through the webbing between the second and third toes of the right hind foot and released.

When working with pods of hatchlings, an effort was made to capture all individuals sighted. I assumed that this resulted in a relatively equal capture effort for successive captures and used the Lincoln Index to estimate the number of hatchlings in a pod. Alligators of all ages became extremely wary when recapture attempts were frequent; therefore, the interval between successive captures of the same pod was usually 3 months. Since pods were usually well separated, locations of different pods could be determined without confusion by visual sightings. Survivorship was calculated by two methods: 1) hatchlings tagged at the initial encounter with a pod were taken as a representative sample, and subsequent recaptures of these initially tagged individuals only were used to determine survivorship; 2) estimates of the number of hatchlings present on a given date were made on the basis of either the Lincoln Index or visual census, whichever was greater.

The movements of 6 alligators on Orange Lake and Payne's Prairie were tracked by radio telemetry. Transmitters of 150-151 MHz with short whip antennae were used. Battery sizes and configurations of the packages varied, but none of the packages exceeded 5% of the body weight

of the alligator instrumented. Two attachment methods were used: 1) steel wires molded into a water-proof instrument package were passed through holes drilled transversely through the nuchal scutes of the alligator; or, 2) straps of nylon elastic and surgical tubing were passed around the body anterior and posterior to the forelimbs.

Longitudinal strips dorsal to the forelimbs prevented the transmitter from sliding ventrally. Instrumented alligators were located at least once every 72 hours.

Data Analysis

All analyses of growth and movement data were done by computer using standard SAS76 statistical packages (Barr *et al.*, 1976). Growth rates were expressed as increment in snout-vent length (SVL) in cm per month or in weight in gm per month, calculated by the following formula:

$$\frac{\text{SVL2 (or Weight 2)} - \text{SVL1 (or Weight 1)}}{\text{Days from capture 1 to capture 2}} \times 30$$

Movement rates were calculated in a similar fashion by substituting distance moved between captures for growth increment.

In order to examine the effects of increasing body size on growth rate, alligators were divided into 3 size classes: class I, < 20 cm SVL; class II, 21-31 cm SVL and class III, > 31 cm SVL. The rationale for these divisions was that they appeared to correspond to alligators from hatching through the beginning of activity the next spring (SVL class I), juveniles from about 0.5 to 1.5 years old (yearlings, SVL class II) and larger juveniles (SVL class III), 1.5 years old or older which had begun significant dispersals (see below). Some variation in growth rate

produced by size was also reduced by expressing growth rates as percent change in initial SVL (or weight) per month.

Observations of winter dormancy in north Florida alligators indicated that little growth probably occurred during this period; food consumption was much lower than during other periods (Deitz and Hines, unpublished data). Recapture intervals of juvenile alligators from different locales varied considerably, and included different proportions of winter days. For example, an alligator captured on 1 May and recaptured on 1 October of the same year had the same recapture interval (5 months) as an animal captured on 1 November and recaptured on 1 April of the next year. Growth increments of these two alligators were likely to be quite different. In order to eliminate this variable when comparing growth rates between locales, the days from 1 April through 31 October were considered to be "growth days," while days from 1 November through 31 March (151 days) were considered to be "no-growth days" and were not counted in the recapture interval. Monthly rates calculated in this manner and then multiplied by 7 compared favorably with annual growth rates calculated for long-term recaptures.

Results

Growth

Growth rates of juvenile *Alligator mississippiensis* from different localities varied considerably (Table 3-1). As expected, the rates decreased at all locales as body size increased. At all sizes, alligators from Orange Lake grew faster in length and in weight than animals from

Table 3-1. Growth rates of juvenile alligators from different north and central Florida locales.

Size Class	Locale	Recaptures	Increase in SVL		Increase in Weight	
			cm/Month	% Change/Mo.	gm/Month	% Change/Mo.
I	Orange L	190	1.80 + 0.67	12.0 + 4.7	33.5 + 29.9	42.0 + 29.9
	L Griffin	86	1.7 + 1.4	11.2 + 9.3	23.4 + 24.5	32.0 + 34.8
	Station Pd	18	1.7 + 1.0	9.9 + 5.4	44.6 + 14.3	43.8 + 13.5
	Payne's Pr	7	0.7 + 0.5	4.7 + 3.7		
	L Wauberg	6	1.3 + 0.8	9.3 + 5.6		
			Orange L, L Griffin and Station Pd > Payne's Pr, p < .05			
II	Orange L	68	1.7 + 1.2	6.5 + 4.7	61.4 + 103.9	23.2 + 30.9
	L Griffin	21	0.6 + 0.9	2.3 + 3.5	20.1 + 20.1	5.9 + 6.3
	Station Pd	6	1.6 + 0.9	6.6 + 3.9	56.6 + 18.3	27.7 + 16.1
	L Wauberg	10	0.7 + 0.8	3.1 + 3.7	51.1 + 25.4	20.4 + 17.4
			Orange L, Station > L Griffin, p < .01 Orange > Wauberg, p < .05			
III	Orange L	12	1.2 + 0.7	3.2 + 2.1	74.4 + 124.7	15.4 + 23.2
	L Griffin	1	0.9	2.6	49.9	7.2
	Station Pd	56	0.5 + 0.6	1.2 + 1.5	102.1 + 172.1	5.7 + 7.8
	Payne's Pr	8	1.2 + 1.2	3.1 + 3.2	15.9 + 132.2	3.3 + 12.7
	L Wauberg	4	0.7 + 0.7	1.6 + 1.6	59.3 + 15.0	4.9 + 1.0
			Orange > Station, p < .01 Orange > Station, p < .01			

other sites, while growth of alligators in Lake Griffin was generally less when compared to all other locales. Growth rates for Station Pond and Orange Lake were comparable except for size class III; Station Pond data were based on captures of more large juveniles (SVL 50-70 cm) than any other areas, which probably biased these rates downward. Growth rates at Lake Wauberg were generally low, although samples were too small for valid comparisons. Differences in water temperatures (Fig. 2-2) and water depth (Table 2-1) which might affect the length of the active season and/or food abundance, did not satisfactorily explain differences in growth rates. Stomach contents of juveniles from Orange Lake and Lake Griffin suggested that in Lake Griffin low availability of aquatic invertebrate prey was limiting to alligator growth (Deitz and Hines, unpublished data).

Data from two 1975 cohorts which were regularly recaptured on Orange Lake (Fig. 3-1) and Lake Griffin (Fig. 3-2) show the actual growth of juveniles for two years after hatching. These and other data from long-term individual recaptures compared favorably with the mean rates calculated from all recaptures within a locale (Table 3-1). Recaptures from October through April supported the assumption that there was no growth in north Florida juvenile alligators during a winter dormancy period of roughly five months, from 1 November to 31 March. This can also be seen in Figs. 3-1 and 3-2.

There were no differences in growth rates between male and female juveniles when tested either within locales or with pooled data from several locales ($p > .05$, t -tests); thus, data from both sexes were combined in preparing Table 3-1. The sex ratio for 264 SVL class II

Figure 3-1. Growth of Orange Lake hatchling alligators, 1975-1977.
Bars represent mean $\pm$ standard deviation.

Figure 3-2. Growth of Lake Griffin hatchling alligators, 1975-1977. Bars represent mean $\pm$ standard deviation.

alligators was 1.45:1 (males:females); for 443 SVL class III alligators it was 1.68:1. These ratios were not significantly different ($p > .05$, Chi-square test) and the sex ratio for all juveniles combined was 1.59:1, or 61.3% males and 38.7% females (Table 3-2).

Survivorship

The survivorship of *A. mississippiensis* from hatching through the end of the first year proved to be surprisingly high for some pods; both methods of calculation provided similar results (Table 3-3). Roughly half of all hatchlings from Lake Griffin and Orange Lake survived the winter, and survivorship after one year averaged approximately .30 (Table 3-3). Mortality for 3 pods in shallow marsh habitats (Station Pond and Right Arm Marsh, Lochloosa Lake) was greater, although differences between lake and marsh survivorship were not statistically significant. Due to the increased dispersal of two-year old animals and, in some cases their learned avoidance of capture techniques, few data were obtained on survivorship from the first through second year. On Orange Lake, survivorship of two pods from 1975-1977 was at least .14 (10/74) based on estimates, or .19 (6/31) based on animals tagged and recovered. On Station Pond 4 (.10) of an estimated 41 animals from two pods were alive after 2 years.

Predation on hatchling alligators was never observed. The wide range of survivorships of different pods suggested that some groups were less susceptible than others, but there were no clear differences in microenvironment, behavior of hatchlings or female attendance (see Chapter 4) between pods with different mortalities. Estimated survivorship of individual pods over 1 year on Orange Lake ranged from 0 to .49;

Table 3-2. Sex ratios of juvenile alligators from different north and central Florida locales.

	Orange L	L Griffin	Station Pd	Payne's Pr	L Wauberg	Other	Total
Males	193	30	126	27	24	46	446
Females	114	34	59	24	18	32	281
%M:%F	63:37	47:53	68:32	53:47	57:43	59:41	61:30

Table 3-3. Survivorship of hatchling alligators through the first year, by locale.

Habitat	Year	Locale	Hatching - 6 Months		#	Hatching - 1 Year	
			Estimated	From Tags		Pods	Estimated
Lake	1975	Orange	.64 (47/74)	.78 (24/31)	2	.31 (23/74)	.52 (16/31)
		Griffin	.52 (62/120)	.58 (19/33)	4	.30 (33/109)	.30 (8/27)
	1976	Orange	.49 (67/136)	.49 (42/85)	5	.26 (35/136)	.28 (24/85)
		Griffin	.43 (51/118)	.40 (18/45)	2	.31 (25/82)	-
	1977	Orange	.41 (43/105)	.32 (10/31)			
	1975-77	Orange	.50 (157/315)	.52 (76/147)	7	.28 (58/210)	.35 (40/116)
Griffin		.48 (113/238)	.47 (37/78)	6	.30 (58/191)	(.30 - 1975 only)	
Marsh	1975	Station	.32 (13/41)	.21 (7/34)	2	.20 (8/41)	.12 (4/34)
		Lochloosa	.41 (7/17)	-	1	.12 (2/17)	-

the range on Lake Griffin was .14 to .56. Temporal patterns of attrition likewise gave no clues to predator identities. All pods showed a reduction in mortality with age, which could be due to increased body size, learning, or both. However, initial mortality was much higher for some pods than for others at the same site. For pods in all habitats attrition during the winter was also less than that observed during the active season. At least 67 of an estimated 88 hatchlings from 5 pods alive in October were alive the next March; this was equivalent to an annual survivorship of .43.

Indirect estimates of mortality from other locales suggested that survivorship of individual pods was quite variable there also. One pod of at least 14 hatchlings had vanished from Lake Wauberg by the following spring, but night counts of 5 other pods in 1977 indicated that 1 year survivorship on Lake Wauberg was probably as high as that on Lake Griffin. Survivorship of two pods from different years at the Carr property were less than .10 and probably 0.

Injuries. The most common injury to small *A. mississippiensis* was loss of the tail tip (Fig. 3-3). Tail tip losses had occurred in 5.1% of my entire sample ($n = 1685$) and accounted for 58% of all injuries. Loss of more than 20% of the tail was recorded in 29 alligators (1.7%), loss of a limb in 21 (1.3%) and severe scarring on head or trunk in 7 (0.4%). The overall injury frequency increased with size of the alligator (Fig. 3-2).

There were substantial differences in the percentage of injuries between localities. Juvenile alligators (SVL < 70 cm) from shallow marsh habitats (Station Pond and Payne's Prairie; $n = 389$) had an

Figure 3-3. Frequency of injuries in alligators from lake and marsh habitats in north and central Florida.

injury frequency of 15.4%; this was significantly higher ($p < .01$, Chi-square test) than the 6.7% injury frequency for all lake habitats (Orange Lake, Lake Griffin and Lake Wauberg; $n = 1096$). Injuries to marsh alligators were also significantly more likely to be severe than those of lake animals, and the frequency of these severe injuries increased with size more rapidly in marsh alligators than in lake alligators.

Growth rates (SVL and weight increments) and movements (see below) of alligators missing only their tail tips were not significantly different from uninjured alligators ($p > .05$, t-tests within all locales). Growth rates for a sample of 11 severely disfigured alligators (SVL > 31 cm) from Station Pond were not significantly different from growth rates of normal alligators.

Movements and Dispersal

The movements of 17 pods in marsh habitat (Payne's Prairie, Station Pond and parts of Orange and Lochloosa Lakes) and 6 pods in lake fringe habitat (Lakes Griffin, Wauberg and Orange) were followed for at least two weeks and usually longer after hatching. Observations were also made on movements of 7 additional marsh and 15 additional lake fringe pods for which the nest locations were unknown. The initial location of a pod after hatching was usually a pool or wallow near the nest, referred to as a "guard pool" by McIlhenny (1935). Females which defended their nests were almost invariably present in these guard pools during incubation (Deitz and Hines, in press), but guard pools were also present at nests which were not regularly attended. On Payne's Prairie

and Orange Lake, 65 of 93 nests (70%) had guard pools located within 3 m of the base of the nest. Most other nests had guard pools within 10 m of the base, connected to the nest site by well-defined trails. Both the presence of freshly smashed vegetation and the increased depth of these pools when compared to the surrounding marsh suggested that guard pools were actively created by the nesting female. Some pools also appeared to have been enlarged by the female just prior to or shortly after her nest hatched.

All alligator nests examined on Orange and Lochloosa Lakes and on Payne's Prairie had a characteristic semicircular excavation after hatching, and it was concluded that all had been opened by the female (Deitz and Hines, in press). Hatchlings were probably led or carried to the guard pool by the female during hatching (Kushlan, 1973; Meyer, 1977) although hatching was never observed. Hatchlings emerging late and/or without the assistance of the parent probably had little difficulty finding the pool because of its proximity, and could also use the vocalizations of other hatchlings as an aid (see Chapter 5). On one occasion, two hatchlings with umbilices still attached were found halfway down the trail leading from the nest to the guard pool 5 m away. The remainder of the pod was in the pool, vocalizing regularly.

The presence and distribution of nest guarding pools, wallows and other sites associated with adult alligator activity were important in determining the movements of pods after hatching. If a guard pool was present, hatchlings in all habitats typically remained in the vicinity of the nest for several days. For 9 such nests, hatchlings spent a minimum of 14.3 ± 10.5 days (range 6-39 days) within 10 m of the nest.

Two other nests that were closely observed had no guard pools nearby, although some water was present at the base of the nest. Hatchlings from these nests spent, respectively, maxima of 5 and 7 days near the nest before moving away. Three additional marsh nests were located adjacent to large pools which appeared to be the female's alligator hole or den site; these pods showed no movement from hatching through the following spring.

After this variable period near the nest, pods began moving away to their overwintering site. The integrity of the pod was maintained throughout these movements, which occurred as regularly-spaced journeys separated by periods during which pods remained in the same pool or series of pools (Figs. 3-4 and 3-5). Displacements of up to 40 m in 24 hrs were recorded; after a long shift in position the pod usually remained stationary for several days. Females were observed moving with their pods in two instances, once during the day and once at night. Parental presence during most other movements was inferred from the fresh trails that connected new locations with the previous ones. Many of the small pools in which pods were found at this time were clearly created or enlarged by the movements of the female. Stands of *Panicum hematomon*, *Pontederia cordata*, *Sagittaria lancifolia* and other soft marsh plants were found smashed down in roughly circular patterns 3 to 5 m across, which created enclosed pockets in the marsh or lake shore.

The dens of three females which nested on Station Pond in 1975-1977 were adjacent to heads or peat islands in the marsh. Trails and pools wound through all of these heads like shallow canyons; hatchlings from two successful nests used these pools for the first two months after

Figure 3-4. Movements of the 75K1 pod, Payne's Prairie.

Figure 3-5. Movements of the 1974 Carr pod.

hatching and intermittently thereafter. Observations of young alligators using heads with similar networks of pools were made at other shallow marshes near Station Pond. Two heads with adjacent pools were known to be used by large males. Neither of these had the extensive network of small pools observed in heads with young; the large pools adjacent to the heads were wider, and the alligator trails present seemed to be straighter. These casual observations suggested that long-term occupancy of a den by a reproductive female alligator might result in permanent habitat modifications related to care of pods.

Most pods reached the den or overwintering site by mid-November. This site appeared to be used extensively by the adult female if it was not actually her den. Total minimum distances moved for 9 marsh pods which were tracked from nest to den averaged 80 ± 34 m (range 25-120 m). The exact route taken was probably more circuitous, as illustrated by the movements of a pod through shallow marsh at the Carr property in 1974 (Fig. 3-5). Though the actual distance from nest to den site was 116 m, the minimum path length for the pod was 445 m, and included two reversals of direction and four stops at different sites before the wintering pool was reached.

Pods on Lake Griffin and on the fringe of Orange Lake showed a slightly different movement pattern. After leaving nests on the fringe of Orange Lake, pods moved gradually out to the edge of open water, and remained there until the onset of cold weather in November; at this point they moved back to a den site in the fringe (Fig. 3-6). Only two nests were located on Lake Griffin, but both of the pods from these nests followed a pattern similar to those on the fringe of Orange Lake. Each year in mid- to late September many pods became visible on the fringe

Figure 3-6. Movements of the 7609 pod, Orange Lake.

of Lake Griffin. If peak hatching is assumed to be at about the same time as on Orange Lake (late August to early September), these pods also must have spent approximately two weeks near the nest before moving away and did not follow a direct route from nest to den.

Hatchlings moved little throughout the winter and, as already noted by Chabreck (1965), were largely inactive except on warm, sunny days. There was some tendency for pods to be extremely closely aggregated during cold weather, and their location in extremely small pockets or pools made them difficult to detect. Two pods observed on Lake Griffin during the winter of 1976-77 were located several meters back from the open water margins of the brushy fringe. Both occupied pools less than 150 cm in diameter. One pod observed on Orange Lake in March 1977 occupied a pool approximately 2 m across. Water temperatures throughout the winter on both Lake Griffin and Orange Lake ranged from 15-20°C (Fig. 2-2). Hatchlings were sluggish at these temperatures, but were capable of coordinated movements and vocalized readily when captured. When disturbed, they dove underneath the floating mats or vegetation into underwater refuges, some of which appeared to be caves used by adult alligators. Some basking took place on Orange Lake during the winter, and hatchlings on Orange and Griffin also fed, although at reduced rates, as indicated by stomach contents (Deitz and Hines, unpublished data). Pods not followed closely during the winter were found in March and April where last seen the previous fall.

Dispersal of alligators following their first winter was documented by periodic recaptures of pods on Orange Lake, Lake Griffin, and Station Pond, with supplementary observations of marked and unmarked juveniles

from these and other locales. The mark-recapture phase of the study, conducted from 1974-77 in conjunction with the Florida Game and Fresh Water Fish Commission, resulted in 559 recaptures of 382 alligators, from a total of 1685 alligators tagged; the majority of these were less than 150 cm in total length.

Representative dispersal patterns of pods of alligators marked on Orange Lake were plotted in Figs. 3-7, 3-8 and 3-9. All three pods demonstrated a one-dimensional spreading along the lake or marsh fringe; dispersal distance after one year was similar for 7 additional pods studied on Orange Lake. Figures 3-7 and 3-8 also illustrate that the center of dispersal was the overwintering site rather than the nest. Seven pods followed on Lake Griffin (Fig. 3-10) showed the same pattern of bi-directional, linear spreading also observed on Orange Lake. However, one-year dispersals on Griffin appeared to be slightly less than on Orange Lake; this was possibly related to slower growth of Lake Griffin juveniles. As expected, dispersal on Station Pond and in marsh areas of Orange Lake was more two-dimensional, but the time sequence of progressively greater displacement from the den site during the first summer was similar.

Pods were still recognizable as discrete aggregations in June of the first year after hatching in both lake fringe and marsh areas of Orange Lake, but they began to lose cohesiveness at about this time. Reaggregation into a single group following a night's feeding (see Chapter 4) no longer occurred, and several clumps of siblings scattered along 100-300 m of shoreline or in different pools in the marsh were

Figure 3-7. Dispersal of the 2172 pod on Orange Lake, 1975-1977.

Figure 3-8. Dispersal of the 2301 pod on Orange Lake,
1976-1977.

Figure 3-9. Dispersal of the 7606 pod on Orange Lake, 1976-1977.

Figure 3-10. Dispersal of 7 marked pods along the shoreline of Lake Griffin, 1975-1977.

observed. Prior to the onset of cold weather in late October many one-year old alligators were solitary, although small groups of siblings were still regularly found.

Some one-year old animals in all habitats demonstrated movement back towards their first overwintering site at the beginning of the second winter. This was evident with pod 2172 on Orange Lake in 1976 (Fig. 3-7). By the end of the summer this pod had dispersed over a shoreline distance of about 330 m. On 27 October 1976, when water temperature had dropped to 19.5°C, 9 individuals from this pod were found together within an area of about 25 m². A return of 1.5 year old alligators to their den site was also observed in 1977 on Station Pond, when severe drought eliminated most of the standing water on the marsh.

Recapture data from hatching through the first year indicated that there was very little migration of alligators from one pod to another, even in situations where pods were relatively close together. The 2172 and 2301 pods on Orange Lake both hatched in 1975, and probably were separated initially by no more than 600 m. Movement early the next spring reduced this separation to about 300 m (Figs. 3-7 and 3-8). However, sibling groups remained distinct until September 1976, when one juvenile from the 2172 pod was captured with the 2301 pod. In October 1976, two alligators from the 2301 pod joined the 2172 group and overwintered with them. These 3 individuals represented 8.6% of the estimated 35 alligators surviving from the two pods for at least one year. No shifts were recorded in 1976-77 for five pods on Orange Lake. Two translocations were recorded on Lake Griffin in 1975-76, representing a total of 6.1% of the estimated 33 one-year survivors from these 5 pods. On Station Pond, 1 of an estimated 8 one-year survivors (12.5%) was from a different pod; this

one animal appeared only after its siblings had vanished, probably through predation. Thus, even where nest densities were fairly high, fidelity to pod or den site was sufficient to support the assumption that aggregations of one-year-old or younger alligators were composed almost entirely of siblings. For areas with low nest densities, the probability that alligators in a group were siblings probably approached 100%.

Dispersal of juvenile alligators following the second winter appeared to be a continuation of patterns of first year dispersal, although fewer data were obtained in support of this. Larger animals dispersed farther than yearlings, as shown by plots of two-year dispersal on Orange Lake and Lake Griffin (Figs. 3-7, 3-8 and 3-10).

Close associations with the natal area appeared to be lost by about the end of the second year on Orange Lake and on Station Pond, as indicated by recaptures and visual sightings of known-age and similarly-sized juveniles. Two-year old alligators remained dispersed at the beginning of their third winter after hatching. Dispersal on Lake Griffin appeared to be slower, possibly as a consequence of reduced growth, but captures and sightings of two-year-olds were few. Two 2-year-old alligators recaptured on Lake Griffin had not moved from their first year ranges. The brushy shoreline and extreme wariness of juveniles from Lake Griffin made recaptures infrequent, and probably biased the sample; dispersal into fringe areas could have occurred, resulting in low probability of recaptures or visual sightings.

A summary of movement rates calculated from recapture data for the three size classes of juvenile alligators appears in Table 3-4. For size

Table 3-4. Rates of movement of juvenile alligators from different north and central Florida locales. Numbers in parentheses indicate number of pods represented.

Locale	Size Class I		Size Class II		Size Class III	
	# Recaps	Rate of Movement (m/day)	# Recaps	Rate of Movement (m/day)	# Recaps	Rate of Movement (m/day)
Orange L	195(16)	0.7 ± 1.4	70(8)	1.6 ± 3.0	12	0.6 ± 1.3
Station Pond	18(2)	0.1 ± 0.5	6(1)	0	57	4.5 ± 8.4
Payne's Pr					8	2.2 ± 4.9
L Griffin	86(8)	0.1 ± 0.5	21(7)	1.0 ± 3.8	2	0
i. Wauberg	6(2)	0	9(2)	3.2 ± 9.4	4	1.3 ± 2.6

classes I and II, only data from Orange Lake and Lake Griffin were sufficient for a useful comparison. Orange Lake alligators moved slightly more than Lake Griffin animals; this difference was significant ($p < .05$, t-test) for size class I. Larger juveniles from both shallow marsh habitats (Station Pond and Payne's Prairie) had higher rates of movement than alligators in the three lake habitats; the difference between Orange Lake and Station Pond was significant ($p < .05$, t-test). Extensive movements (over 1000 m between successive captures) by some juveniles in size class III from all habitats suggested that movement rates calculated for this size class were substantial underestimates. The extremely low rate of movement obtained from recaptures on Orange Lake probably reflects some bias in collecting, since not all areas of the lake were visited equally. Capture efforts on Station Pond were more evenly distributed. The longest movement recorded in the study was for alligator 20103, a male 82 cm in TL at initial capture. This alligator was captured in the southwest corner of Lochloosa Lake on 7 October 1975, and was recaptured on 17 September 1976 on the east shore of Orange Lake after moving a minimum distance of 5100 m in 346 days (14.7 m/day).

Movements of males and females were not significantly different at any of the localities studied. This was not unexpected for alligators in their first year, since these individuals were still in pods. However, larger, more solitary juveniles also demonstrated no sex-related differences in rates of movement. In the largest recapture sample from Station Pond, movement of males and females was identical (4.5 ± 7.8 m/day vs. 4.5 ± 9.7 m/day for 39 male and 18 female recaptures,

respectively). Data for males and females were combined in the above comparisons of movement rates between locales.

Alligators tracked by radio telemetry moved very little, with one significant exception (Table 3-5). However, instrumentation periods were too short for valid comparisons with mark-recapture data. Movements of alligator 20337 on Orange Lake (Fig. 3-11) suggested that two year old alligators may sometimes travel extensively, and that movement rates calculated from recaptures were low estimates of actual travel. Number 20337 was probably beginning its third year; the distance it moved in 20 days exceeded the maximum dispersal through the first 2 years for all members of the 2172 or 2301 pods on Orange Lake (Figs. 3-7 and 3-8).

Two instrumented alligators were subsequently recaptured after their transmitters had failed. The sites of both recaptures suggested that the data obtained during telemetry were representative of the later movements of these individuals. Alligator 20145 was largely sedentary on Payne's Prairie from 23 April to 21 May 1976. It was recaptured on 14 July 1976 approximately 200 m from its last contact, having moved an average of 3.7 m/day in the interim. Its weight had increased 210 gm (26% initial) from 19 April to 14 July, indicating that food was readily available and that the transmitter package (which was still attached) had not interfered with feeding. Contact with alligator 20089 was lost on Orange Lake on 21 October 1976, and regained when the individual was recaptured 60 m from its last known location on 16 March 1977. Weight loss in the interval was 7%, which was consistent with winter weight losses recorded for juveniles of similar size, and the recapture location suggested that little movement had occurred over the winter.

Table 3-5. Juvenile alligators followed by radio telemetry.

Number	Sex	Total Length (cm)	Wt. (gm)	Probable Age (yrs)	Location	Dates Instrumented	Rate of Movement (m/day)	Distance from Initial Capture Site to Last Contact (m)
2257	-	41	164	1.2	Payne's Pr	31 Oct. - 3 Nov. 75 3 days	0	0
20108	-	56	409	1.2	Payne's Pr	31 Oct. - 6 Nov. 75 6 days	10.0	60
20145	F	71	810	2.5	Payne's Pr	23 - 26 Apr. 76, 3 - 21 May 76. 21 days*	8.6	20
20089	F	88	1690	2.2	Orange L	15 Oct. - 21 Oct. 76 6 days*	38.3	90
20337	M	92	2020	2.2	Orange L	15 Oct. - 4 Nov. 76 20 days	99.0	1360
20385	M	108	3600	4.5	Orange L	8 Apr. - 22 Apr. 77 14 days	8.6	120

* Subsequently recaptured.

Figure 3-11. Movements of alligator #20337, followed by radio telemetry on Orange Lake.

Discussion

The effects of habitat on growth rates of juvenile *A. mississippiensis* are presumably related to food availability. Prey of small *A. mississippiensis* consists largely of macroinvertebrates and fish (Fogarty and Albury, 1967; Chabreck, 1971; Deitz and Hines, unpublished data). The abundances and availability of these items must vary considerably with water temperature, water depth and trophic state of the habitat. Captive studies of young *A. mississippiensis* have documented the relationship between food availability and quality (measured via protein conversion rates) and growth rate (Coulson *et al.*, 1973; Joanen and McNease, 1974). Food consumption by young alligators from brackish marshes is less than that of alligators from fresh marshes, probably leading to slower growth (Chabreck, 1971).

Growth rates of juveniles from other portions of the range of *A. mississippiensis* are compared with those from north and central Florida in Table 3-6. The high rates observed for south Florida alligators presumably result from a reduction in or elimination of the winter dormancy period (Hines *et al.*, 1968). Orange Lake alligators growing for 12 months at the same rates observed for the 7 month active season would have an annual increment in total length of approximately 36 cm--roughly the same growth as Everglades animals. Seasonal influences on growth are also illustrated by Murphy's (1976) data from South Carolina, where juveniles grew faster in artificially heated portions of a lake than in unheated parts (Table 3-6). Prey availability is undoubtedly quite variable both within and between locales, as well as seasonally.

Table 3-6. Growth rates of *Alligator mississippiensis* throughout the southeastern U.S.

Location	Annual Size Increment (cm/yr)	N	Source
S. Florida - Everglades	34.1	33	Hines <i>et al.</i> , 1968
Louisiana	31	38	McIlhenny, 1934
N. Florida - Orange L.	21.1	270	This study.
N. Florida - Station Pond	15.9	80	This study.
N. Florida - L. Griffin	11.9	108	This study.
S. Carolina - Par Pond	15.9	*	T. Murphy, 1976
S. Carolina - Par Pond, heated	21.0	*	T. Murphy, 1976
S. Carolina	16.1	22	Bara, 1972

* Sample size for all Par Pond animals was 53.

Growth rates for most other crocodilians have not been determined. Growth rates (converted to increment in total length) of *Crocodylus porosus* in northern Australia averaged about 36 cm/yr for males and 33 cm/yr for females (Webb and Messel, unpublished data). Seasonal variations were not as pronounced as in *A. mississippiensis*. Rates for *C. niloticus* from east Africa reported by Cott (1961) from various sources were slightly below the 31.7 cm/yr increase in total length determined for captives. Other data for *C. niloticus* from Graham (1968) suggest that sub-optimal habitat reduces growth considerably.

Males grow faster than females in *Crocodylus porosus* (Webb and Messel, unpublished data), *C. niloticus* (Graham, 1968) and *A. mississippiensis* (McIlhenny, 1935). Differences in growth rates of Louisiana *A. mississippiensis* are probably not significant until juveniles reach at least 60 cm SVL (Nichols *et al.*, 1976). My data suggest similar conclusions for Florida alligators. Juvenile alligators are sometimes difficult to sex; Hines *et al.* (1968) have reported 80% males in their south Florida sample, a figure which they believed to result from sexing errors. The sex ratio determined for north Florida juveniles (1.59:1) is in excellent agreement with the sex ratios of Louisiana adults (1.51:1 - Chabreck, 1966).

Survivorship of juvenile crocodilians is unknown, but has been widely assumed to be low. Popular and semi-technical accounts of *A. mississippiensis* report mortality to be 90% or more for the first year (Neill, 1971); the few data available indicate that it may be significantly lower. My estimates probably represent minimum figures for survivorship, since many juveniles which were known to be alive

(subsequently captured) were not captured or seen on some visits to their pods. The two-year survival of 2 pods in South Carolina was approximately .16 (Murphy, 1976), which is comparable to my figures. Nichols *et al.* (1976) estimated one-year survivorship of Louisiana alligators to be .35 and two-year survivorship to be .21, although no supporting data were provided for these estimates. The survivorship of one Louisiana pod marked in 1921 was apparently at least .66 through 1927 (McIlhenny, 1935). Quantitative data on survivorship in other crocodilians are available only for *Crocodylus porosus* in northern Australia, where the one-year survivorship of one cohort of 58 hatchlings was at least .40 (Webb, 1977). Observations by Graham (1968) for *C. niloticus* indicate that where habitat is unsuitable for juveniles (bare shoreline) mortality may be nearly 100%.

While not statistically significant, the differences in survivorship between habitats suggested differences in predation. This is supported by the frequency of injuries, which, like mortality, was highest in shallow marsh habitats. This pattern implies that wading birds are an important predator; their access to small alligators is probably much better in shallow marshes than in deep water areas. Wading birds are known predators of other juvenile crocodilians such as *Crocodylus niloticus* (Cott, 1961) and *C. palustris* (Dharmakumarsinhji, 1947), and have been observed preying on juvenile alligators at the Carr pond (Carr, pers. comm.). Droughts are more likely to increase mortality of marsh alligators above that of lake alligators (Nichols *et al.*, 1976); this could be by desiccation or result from increased access by predators. Drought mortality of subadults on Station Pond

in 1977 was severe (Hines, Woodward, and Deitz, unpublished data), and Staton and Dixon (1975) attributed low survivorship of some *Caiman crocodilus* in Venezuela to drought.

An age-related increase in the natural incidence of injuries similar to that observed for *A. mississippiensis* appears to be typical for other juvenile crocodilians as well. Injuries to hatchlings and juveniles less than about 1 m in total length have been assumed to represent predation, while injuries to larger juveniles and adults are attributed to social interactions and, possibly, attempted cannibalism (Webb and Messel, 1977; Staton and Dixon, 1975). Fluctuating water levels concentrate *Caiman crocodilus* populations and increase social conflict (Staton and Dixon, 1975, 1977); this could account for the higher frequency of injuries in marsh-dwelling *A. mississippiensis*. However, alligator population densities on Orange Lake and Lake Griffin were as high or higher than on Station Pond (Hines, Woodward and Deitz, unpublished data), and the high incidence of injuries on Station Pond was recorded prior to the 1977 drought. Evidence for significant cannibalism in *A. mississippiensis* is likewise poor, as will be discussed below (Chapter 5).

The movements of juvenile *A. mississippiensis* in north Florida correspond closely to those of Louisiana alligators with respect to movement from nest to den, overwintering, and the initiation of dispersal the following spring (McIlhenny, 1935; Chabreck, 1965). Chabreck (1965) has also described reduced movement of pods when nests are located adjacent to dens, as well as the movement of pods to open water when nests are situated nearby (similar to my lake fringe nests).

The importance of the female's guard pool or wallow in determining post-hatching movements has not previously been emphasized. In addition to possibly providing deeper (and cooler) water for the adult during attendance of nests and young, the wallows may be important in providing a small but locatable refuge in which young can assemble after hatching. Pools created by females during movements of the pod to the den may similarly aid in assembly, and function to minimize losses of stragglers. While these pools could increase the chances of predator detection, particularly by wading birds, this may be offset by the increased visibility of young which they provide the attending parent. Smashed vegetation provides basking sites for the hatchlings; in some areas of marsh these are not readily available. Hatchlings in pools are also able to disperse more during nocturnal feeding without entering dense vegetation (see Chapter 4); this may facilitate foraging by increasing range and also by improving access to insects which would otherwise be unobtainable on plant stems above the water.

Dispersal of juvenile alligators during their first summer, followed by returns to the den during the second winter or during droughts, has also been reported by Chabreck (1965) for Louisiana and by Fogarty (1974) for the Everglades. From comparisons of Lake Griffin and Orange Lake, I suspect that pod dispersal is related to size in all habitats and occurs more slowly if growth is retarded. However, mean movement rates computed for individual recaptures (Table 3-4) did not correlate well with growth rates. Movement rates of size class III juveniles indicated that alligators of this size have lost permanent contact with their natal areas.

Movement of immature alligators in Louisiana decreases from spring through fall, with males exhibiting slight preferences for open water areas and females for marsh (McNease and Joanen, 1974; Taylor *et al.*, 1976). Both sexes show wide variation in daily movement, and occasional long movements (1 km) are regularly observed. My observations of juvenile movements based on recapture data from Florida are consistent with these patterns. Sex-related differences are not evident in small juveniles in Florida; the juveniles tracked by McNease and Joanen (1974) were larger (mean SVL 73 cm), which is probably significant.

Wallows or guard pools are also used by nesting female *Crocodylus porosus*; the photograph by Webb *et al.* (1977) of a nest in northern Australia shows wallows which appear identical to those used by *A. mississippiensis* on Orange Lake. Small pools are also reportedly used by adult *C. palustris* (Dharmakumarsinji, 1947) and *C. niloticus* (Cott, 1961) in caring for their young. For *C. niloticus*, use of these pools may require overland movements of female and young from river bank nests to suitable inland sloughs (Cott, 1961). The semi-permanent habitat alterations produced by *A. mississippiensis* in making dens and trails (McIlhenny, 1935; Craighead, 1968) have not been reported for other crocodilians, although *C. niloticus* and *Caiman crocodylus* will deepen pools in response to drought (Cott, 1961; Staton and Dixon, 1975). Parental care is sufficiently widespread in crocodilians (see Chapter 4) that permanent nursery areas such as those used by Station Pond alligators may be formed by the reproductive activities of other marsh-dwelling species.

Australian *Crocodylus porosus* form creches (= pods) after hatching, and in some cases these are moved or accompanied by an adult (presumed parent) for several weeks (Webb *et al.*, 1977). Subsequent dispersal of *C. porosus* hatchlings occurs earlier than in *A. mississippiensis*, and distances moved by one- and two-year old juveniles are much greater (Webb and Messel, 1978). Tidal currents in the rivers where these groups were studied are evidently significant, since there is some tendency for animals to disperse downstream (Webb and Messel, 1978). Medem (1971a, b) has suggested that *Paleosuchus palpebrosus* hatchlings, which generally occupy swift streams, also disperse rapidly without forming large pods. Occasional long distance movements similar to those observed in individual *A. mississippiensis* also occur in juvenile *C. porosus*, and these have been postulated to represent excursions which are followed by returns to a core area (Webb and Messel, 1978). Juvenile *A. mississippiensis* apparently possess homing abilities sufficient to allow such returns (Chabreck, 1965; P. Murphy, 1978; G. Rodda, unpublished data).

CHAPTER IV SOCIAL BEHAVIOR OF JUVENILE ALLIGATORS

Introduction

The recent world-wide interest in crocodilian conservation has resulted in many new observations of crocodilian behavior. Enough information on adult social behavior has accumulated for 3 species (*Alligator mississippiensis*, *Crocodylus acutus*, and *C. niloticus* to support valid interspecific comparisons (Garrick and Lang, 1977), although comprehensive field studies of adult behavior such as Modha's on *C. niloticus* (1967) are still lacking. Attempts to breed most crocodilians in captivity have produced surprising new data on nesting and parental care (e.g., Alvarez del Toro, 1974; Hunt, 1975; Pooley, 1977) and suggest that recently discovered behaviors such as parental transport of young in the mouth may be a consistent feature of the order.

Descriptions of juvenile social behavior in crocodilians usually have been confined to observations that the young of most species remain in groups for some period after hatching. Vocalizations have been presumed to be important in maintaining these groups (Campbell, 1973), but the actual maintenance behaviors and duration of groups have not been systematically studied. While some parental care of groups of young has been regularly observed in captivity, the consistency, duration and significance of parental care in wild crocodilians are largely unknown. Parental care for 5 weeks after hatching has been reported for *Crocodylus*

acutus by Alvarez del Toro (1974); Cott (1971) has observed 12 weeks of post-hatching care in *C. niloticus*.

McIlhenny's (1935) observations of *A. mississippiensis* indicated that pods persisted until the following spring, suggesting that they were actively maintained, and were protected by the parent female throughout this period. These observations were impugned by Neill (1971). However, both Chabreck (1965) and Fogarty (1974) also reported pod persistence for one year, and Kushlan (1973) provided unequivocal evidence for maternal protection of the young. The objectives of this portion of the study were to obtain additional data on the social behavior of pods and the frequency of parental care and, by examining pods in different locales, to determine the extent to which these might vary with habitat. The significance of vocalizations in maintaining pods and mediating parental care was also investigated.

Methods

General locations of pods were determined as in Chapter III. Diurnal observations of pods were usually made with binoculars from within 10 m; small alligators could be observed successfully without a blind from this distance if observer movements were reduced to a minimum. Temporary blinds were occasionally used, but frequent position shifts by pods made their regular use impossible. Juveniles were also successfully observed from an airboat seat; it appeared that movements made high (2 m) above the water surface were not easily detected. Detailed observations of nocturnal behavior proved impossible. Passive night vision equipment (starlight scope) was used on several

occasions, but resolution and image intensity were both too poor to distinguish juvenile alligators from emergent vegetation. General movements and behavior of juveniles after dark were recorded by flashing a headlamp beam at regular (usually 15 minute) intervals and noting positions and any other activity of alligators visible. Eyeshines (reflections from the tapetum lucidum) were helpful in locating alligators in dense cover. Flashes of 15 seconds or less appeared to have little effect on movements or rates of vocalizations; longer flashes seemed to produce some avoidance and cover-seeking behavior and were avoided. Some nocturnal observations were made by covering a headlamp with a red filter (auto taillight cover). This light had limited range and produced dim eyeshines at best, but it was also far less disturbing. Many individuals appeared entirely unaffected and continued to move and feed in an apparently normal fashion while the red light was on.

Positions of individual juvenile alligators during the day were recorded at regular intervals. Each animal was scored as: 1) moving or stationary; 2) on land or in the water; 3) in the sun or shade; and 4) under cover or in the open, *i.e.*, relatively exposed when viewed from above. Verbal descriptions of important physical features as well as field sketches were made to assist in plotting movements. Individual recognition was possible for some juveniles that had anomalies in their banding patterns.

The vocalizations produced by hatchling alligators have been referred to as grunts by Campbell (1973) and Herzog and Burghardt (1977). These grunts were quite audible at most distances from which I observed pods. Grunts frequently occurred in bursts of one or more single grunts

produced in rapid succession by one individual; following Herzog and Burghardt (1977) each of these groups of grunts was counted as a single series. The number of vocal series produced during each 10 or 15 minute period was tabulated; if the individual vocalizing was seen, context was also recorded. Each pod received a score for number of vocal series/alligator-hour (VAH) for each period, calculated in the following fashion:

$$VAH = \frac{\# \text{ vocal series during the observation period}}{(\# \text{ juveniles known to be present})(\text{period length in hours})}$$

Differences in frequency, intensity and location between vocalizations of different individuals were such that scoring was difficult only if a large number of individuals were vocalizing simultaneously. Tape recordings of vocalizations were made with an AKG 451E directional microphone and a Nagra III B or Tandberg Model 11 tape recorder, and analyzed with a Kay Sonagraph (Model 7029A).

Results

Activity Cycle

At sunrise, small alligators were in the water, usually in dense cover such as emergent *Cladium* or *Pontederia* stands. Little activity was evident at this time; those alligators which were visible remained motionless and seldom vocalized. Emergence from cover began about one hour after sunrise (Figs. 4-1b and 4-2b), and appeared to depend on illumination by the rising sun of portions of the small coves where hatchlings were located. Prior to emergence, a few juveniles would begin to swim about and emit low intensity juvenile grunts. The number

Figure 4-1. Morning emergence by hatchling alligators in Orange Lake.

Figure 4-2. Morning emergence by hatchling alligators on Payne's Prairie.

of grunts by seen and unseen hatchlings rose rapidly at this point (Figs. 4-1a and 4-2a). As most alligators in a group began to vocalize sporadically, the first few individuals emerged from cover and climbed out of the water onto tussocks or clumps of vegetation in the sun, grunting regularly as they did so. The rest of the pod followed immediately, climbing out into the sun while grunting. Most of these hatchlings used the same tussock or clump of weeds as the first individuals to emerge. Alligators ceased vocalizing once they had climbed out of the water and moved onto a suitable basking spot. At the time of emergence, site air temperatures were almost always equal to or greater than water temperatures.

The movement of the group from aquatic cover to terrestrial basking sites usually took less than 30 minutes and was often completed in 15 minutes (Figs. 4-1 and 4-2). As indicated above, alligators oriented to basking spots already occupied by other pod members, even though there were often many other apparently suitable sites nearby. This resulted either in one large aggregation of basking alligators within an area sometimes as small as 1 m^2 , or if small clumps of emergent vegetation were being used, in two or three smaller groups adjacent to each other. Hatchlings that remained in the nursery pool by the nest frequently basked on the base of the nest; those which had moved into other pools used vegetation which had been flattened down by the female's body. If the female was present and remained stationary in the sun, hatchlings sometimes used her head and back as basking sites.

Cloudy skies or cool temperatures delayed or inhibited this coordinated morning emergence. I made no systematic observations of

pods in mid-winter but hatchlings which were observed basking at this time of year were as tightly bunched as on other occasions.

Following morning emergence, juvenile alligators basked for varying periods; the duration of those was probably dependent on individual thermoregulation. For most hatchlings, the period on land lasted about 2-2.5 hours, and included movements between sun and shade (Figs. 4-1b and 4-3). Little movement and few vocalizations were evident in the group during this period; VAH for 8 pods observed on 14 sunny days averaged 2.3 ± 1.7 . Alligators were quite tolerant of being stepped on or jostled by other juveniles while basking, and it was not uncommon to see individuals basking with the heads or tails of others lying across their backs. Some hatchlings appeared almost comatose, and were observed to lie motionless and fully exposed to the sun for 30 minutes or more with their eyes closed. Hatchlings would also occasionally climb up the stems of emergent vegetation, especially *Cladium jamaicense*, while basking, and I observed some that had climbed more than 30 cm above the water surface.

After basking, hatchlings moved into shady areas on land or in the water (Fig. 4-4). These movements were accompanied by sporadic vocalizations. While movements off of the basking platforms were not as concerted as emergence, most alligators left within about 1 hour of one another; this usually took place from 4 to 5 hours after sunrise (see Figs. 4-3 and 4-4). Overheating may have been the principal stimulus for these movements, since the alligators selected cooler areas and air temperatures at this time often exceeded 30°C. However, I rarely observed obvious behavioral thermoregulatory responses, such

Figure 4-3. Percentage of hatchling alligators in the water at different times of day.

Figure 4-4. Distribution of hatching alligators under cover or basking during the morning hours.

as postural adjustments, that would support this supposition; gaping was only rarely observed. Some hatchlings and larger juveniles yawned briefly once or twice before entering the water, but this also was infrequent.

During warm weather, young alligators spent most of the remainder of the day in the water, generally remaining under the cover of floating or emergent vegetation and moving occasionally. As noted above, basking was prolonged in cooler weather. Throughout the afternoon some alligators climbed out of the water to bask briefly or to lie in the shade, but there appeared to be no group coordination to these movements and most pod members remained in the water (Fig. 4-3). Short movements by individuals gradually dispersed the pod as the day progressed, and the hatchlings were never as densely aggregated as during the morning basking period. Vocalizations were few; VAH for the midday - sunset period averaged 2.4 ± 1.3 . Although alligators were relatively inactive, they responded readily to potential prey and feeding strikes were regularly observed at all hours. By sundown, all individuals in a pod were normally in the water, under cover and largely motionless.

Immediately after sundown there was an increase in activity which duplicated the morning emergence in its rapid, synchronous onset. The number of alligators moving and grunting rose steeply over a 15 minute period, and as these juveniles began swimming around they also emerged from cover. Figs. 4-5 and 4-6 are representative temporal plots of the rate of vocalization by the pod (VAH) and number of alligators visible to me. In Fig. 4-5 grunting peaked before most of the pod became

Figure 4-5. Evening emergence of the 77033 pod, Orange Lake.

Figure 4-6. Evening emergence of the 77-IE pod, Orange Lake.

visible--it appeared on this occasion and others that hatchlings began swimming about while vocalizing and then emerged from cover. An increase in feeding strikes was also associated with these increased movements and feeding continued as the pod rapidly dispersed. Alligators vocalized as they moved, and for the first hour after sunset mean VAH was 8.8 ± 6.9 , significantly higher than mean VAH observed for the morning or afternoon ($p < .01$, t-test). Thereafter, vocalizations declined; this was coincident with a decrease in feeding activity and swimming movements.

Figures 4-7 and 4-8 are representative plots of the positions of most of the members of one pod on Orange Lake during nocturnal emergence. The rapid dispersal following emergence is evident. The limits of dispersal were approximated by the end of the first hour after sunset, although some individuals continued to move away from the center of the group for the next few hours. By 0030 hours feeding activity had ended, and alligators had moved into or adjacent to vegetation along the nearest shoreline (mostly *Hydrocotyle umbellata* in Fig. 4-7). Little additional activity was seen until 0445 hours when the hatchlings began returning to their initial emergence point, disappearing into the vegetation when they arrived. In contrast to most other movements, these were not accompanied by an increase in vocalizations. By 0615 the distribution of the pod had contracted to a 20 m strip of shoreline and a small cove (Fig. 4-8); this was a normal scatter for hatchlings in the morning prior to emergence.

On subsequent nights, the pod depicted in Figs. 4-7 and 4-8 deployed over approximately the same area each evening, and regrouped

JUNE 5, 1977
SUNSET at 2026

Figure 4-7. Evening deployment of foraging juvenile alligators on Orange Lake (continued on Fig. 4-8).

JUNE 6, 1977

Figure 4-8. Return of foraging juvenile alligators to their initial emergence point on Orange Lake (continuation of Fig. 4-7).

in the same refuge the next morning. Concurrent observations of 3 other pods on Orange Lake indicated that this was a typical pattern. Observations on Lake Griffin were not as detailed; however, pods there did show the same sort of expansion early in the morning followed by a retreat under cover and, still later, a contraction in area covered by 0200 hours. Small alligators on Lake Griffin did not venture as far from shore as similarly-sized animals on Orange Lake, possibly because weedy cover was not as abundant.

Water depths at the site of Fig. 4-7 and 4-8 and in marshy areas where other pods were located were usually 60 cm or less. These shallow areas cooled rapidly at night, and were often below 25°C before midnight. This drop in water temperature was probably one factor influencing the reduction in feeding activity of small alligators. However, reduced feeding activity after midnight was also observed in pods located in deeper water areas of Orange Lake and Lake Griffin, where water temperatures remained above 28°C throughout most of the night during the summer months.

Alligators did not exhibit nocturnal dispersal for the first few weeks following hatching, but did spread out at night once they reached larger pools in the marsh or lake shoreline. Pods expanded more at night as individual body size increased. Hatchlings in October following hatching, SVL 14-17 cm, were rarely found more than 10 m from cover and the maximum spread of a pod at night did not exceed 20 m of shoreline. Pods appeared to disperse more each night as air and water temperatures increased in the spring, and by June dispersals such as that shown in Fig. 4-7 and 4-8 were typical. Most juveniles in all habitats measured 19-23 cm SVL at that time (see Chapter III).

Pod cohesion began to disappear in mid to late June of the year following hatching, although this was a gradual phenomenon (see Chapter III). There were no consistent individual associations in the sub-groups formed at this time. Some social basking in the morning was observed, but not all individuals basked in the same small area, and vocalizations during emergence were much reduced; the latter was also true for nocturnal emergence. Distributions of juveniles in all localities following their second winter suggested solitary behavior, although these alligators were much warier and harder to observe during the day than younger juveniles. The activity of these larger juveniles appeared to be about the same as that of hatchlings, without the same level of group coordination; juveniles emerged from cover in the morning to bask, returned to the water and moved little throughout the day, and finally emerged at sundown to feed.

Vocalizations

Juvenile grunts were emitted by hatchlings in a variety of contexts. As discussed above, increases in the average number of vocalizations by individuals in a pod were associated with morning and evening emergences from cover. While these synchronous emergences produced the most striking changes in rates of vocalization, grunting increased in almost every situation which involved increased movement by and/or disturbances to the pod. Such situations included: the arrival, departure or movement of an adult alligator through the pod; increased movements associated with feeding; separation of individuals from the pod; and artificial disturbances created by my observations or manipulations.

Context for many grunts was not recorded because it was frequently difficult to determine which of several alligators in a small aggregation had vocalized. The association of grunting with movement was pronounced. Of 589 vocal series produced by undisturbed pods, 67 (11.4%) were given by stationary hatchlings, 273 (46.3%) were given by moving alligators, and 249 (42.3%) were given by alligators which were either moving or adjacent to moving animals (*i.e.*, the identity of the vocalizing individual in this last category was uncertain, but the vocalization was associated with movement by a juvenile alligator). Hatchlings on land rarely vocalized except when emerging from or entering the water, and VAH during daylight hours was positively correlated with the proportion of alligators in the water ($r = .43$, $p < .01$, $n = 55$ observation periods).

The increases in VAH observed during both morning and evening emergences were associated with increased swimming activity and other movements by individual hatchlings in the pod. The vocalizations produced during morning emergence appeared to attract pod members to a single area where a synchronous emergence followed by basking took place (social bask). Basking individuals were stationary, and vocalized infrequently.

During evening emergence, individuals grunted frequently as they dispersed and continued to grunt irregularly as they foraged. Single grunts rather than vocal series of two or more grunts were often emitted by these foraging juveniles; there was a significant difference in the number of grunts per series between alligators vocalizing during the day and those vocalizing at night (Fig. 4-9).

Hatchlings that made feeding strikes during the day would also grunt while foraging. Foraging movements and grunting by these alligators

Figure 4-9. Number of grunts/series emitted by juvenile alligators during the day and at night.

were sometimes followed by similar behavior in nearby juveniles. One hatchling which had captured a large sphinx moth (*Sphingidae*) larva was pursued for more than 5 minutes by two other juveniles that grunted repeatedly. One of the pursuers succeeded in obtaining a piece of the larva. During the chase 10 additional hatchlings emerged from cover; most of these individuals began foraging as they emerged.

There was one significant exception to the generalization that juvenile alligators increased their rate of vocalization while moving. During reaggregation just before dawn following the previous night's dispersal (Fig. 4-8), juveniles returned to their emergence point in silence. Some juveniles also responded to disturbances after dark by moving silently under cover; these movements were also directed toward the initial emergence point, and nocturnal disturbance of a dispersed pod generally resulted in a net reduction in the area occupied by the pod as members all returned to the same area.

During the daily movements of the pod, hatchlings often became separated from the main group, sometimes by as much as 10 m. In the dense cover occupied by most pods, this resulted in loss of visual contact. Vocalizations by isolated juveniles would often be answered by one or more alligators in the main group. If answered, isolated individuals lifted their heads and oriented them toward the response. They would then begin to move toward the rest of the pod, grunting as they moved; their vocalizations usually received answering grunts. Isolated hatchlings continued moving and grunting until they had rejoined the pod. To test this ability to locate pods under field conditions, I released three hatchlings (on separate occasions) 10-15 m

away from non-sibling pods in locations unfamiliar to the released juveniles. All three hatchlings correctly oriented to grunts produced by members of the pods and moved directly toward them, vocalizing as they did so. Dense emergent vegetation in all three areas made visual contact by individuals more than 2 m apart extremely unlikely, and vocalizations appeared to be the only clue used by the transplants in locating the new pods. After joining the pods, at least 2 of the 3 released juveniles remained with them, for a minimum of 2 weeks and 9 months, respectively.

The arrival of what appeared to be the parent female alligator also resulted in brief increases in grunting by the pod, and I was frequently alerted to the presence of an adult alligator by the grunting of the juveniles. Movements of the female while with the pod also provoked grunts. During my only daylight observation of a female moving with her pod, the hatchlings were vocalizing regularly as they followed her.

Pods that detected my approach during the day responded by grunting rapidly and retreating into nearby cover, often submerging as they swam away. Response to predators was assumed to be similar. No group coordination was evident, and the pod normally became scattered as a result of such disturbances. Continued disturbance of pods after dark also resulted in scattering of individuals. Juveniles normally re-emerged from cover 15-30 minutes after the disturbance had ceased. These emergences were very similar to those of morning and evening, in that decreased grunting preceded the actual movement of individuals out of weedy cover. Hatchlings continued to grunt as they emerged, and responded to vocal or visual contact with siblings by moving toward them; this resulted in a reaggregation of the scattered pod.

If basking had been interrupted by the disturbance, most juveniles returned to land.

Various stimuli increased the intensity and rate of grunting by individual juveniles. Individuals which were swimming slowly about or foraging emitted soft, infrequent grunts such as those represented in Fig. 4-10, while hatchlings responding to my approach or the approach of an adult alligator produced louder grunts, such as those in Fig. 4-11, at a more rapid rate. These variations between grunts in different contexts were continuous, and as noted by Herzog and Burghardt (1977) the grunt appears to be a graded signal. A difference in frequencies is also evident from a comparison of Figs. 4-10 and 4-11. Grunts emitted at greater intensities began at higher frequencies before a rapid down-sweep, and harmonics were more evident. The most intense and most rapidly repeated grunts were those emitted in "distress" contexts (Fig. 4-12; see also Herzog and Burghardt, 1977, Fig. 2). This "juvenile distress call" has been referred to as distinct from the grunt by several authors (*e.g.*, Neill, 1971; Herzog and Burghardt, 1977; Staton, 1978). However, I was unable to detect consistent differences between sonagrams of grunts recorded in distress contexts and grunts recorded in other contexts, including those produced prior to hatching (Fig. 4-13); furthermore, experimental evidence (see below) indicated that juvenile alligators had similar difficulties. For convenience, these high-intensity, rapidly repeated grunts were referred to as distress calls by virtue of the context in which they were often emitted--not because of any unique characteristics of the signal (see Campbell, 1973).

Figure 4-10. Sound spectrograph of low-intensity juvenile grunts of *Alligator mississippiensis*, SVL 12-13 cm.

Figure 4-11. Sound spectrograph of high-intensity juvenile grunts of *A. mississippiensis*, SVL 12-13 cm.

Figure 4-12. Sound spectrograph of calls of a hand-held juvenile *A. mississippiensis*, SVL 12 cm (distress context).

Figure 4-13. Calls of an unhatched *A. mississippiensis* from an egg.

Distress calls were emitted in rapid succession when juveniles were alarmed by my approach and when they were captured. In some instances, they resulted in the approach of adult alligators, assumed to be the female parents (see below). The behavior of other juveniles upon hearing calls emitted in these contexts was quite variable; my observations were complicated by the fact that it was often impossible to determine whether the alligators were responding to the distress calls or to the original disturbance. Many juveniles, whatever their subsequent behavior, vocalized in response to distress calls (as did many in response to juvenile grunts). Some juveniles appeared to be alarmed, and responded by submerging or by swimming or running into cover. Others responded by moving toward the source of the calls. This last response was so consistent that it was sometimes useful in capturing juvenile alligators. Distress calls of captives could be elicited by squeezing them or by agitating the bag in which they were being kept; many of the remaining pod members would then emerge from vegetation and approach. Older juveniles could also be attracted in this fashion, although not as regularly as hatchlings. Submerged hatchlings surfaced in response to calls of hand-held siblings, indicating that the calls were audible underwater.

Although vocalization appeared to be of great importance in maintaining pod cohesion, visual contact was clearly an important close range signal. Moving hatchlings were often followed closely by other hatchlings. As noted above, the first hatchlings to emerge from cover in the morning were followed by the remainder of the pod. Juveniles normally swam with only a small portion of their back exposed; they

were never observed to inflate sufficiently to expose more than this. The distal half of the tail was allowed to protrude, so that both the head and tail of hatchlings which were swimming or resting in the water were visible above the surface. This posture was identical to the head-emergent tail-arched posture described by Garrick *et al.* (1978) for adult *A. mississippiensis*. In hatchlings, the posture was probably used to increase visibility of individuals to other pod members or to the parent; it appeared to have no other social significance. The tail was submerged and only the head was visible when hatchlings were alarmed or concealed under cover.

No structured social organization was evident in pods. Those which emerged first to bask were different individuals from day to day. Hatchlings were extremely tolerant of close contact. An individual would occasionally grunt if stepped on, but more frequently would either ignore the disturbance or move over.

By July of their first year pods of juvenile alligators were much warier of my approach and more difficult to observe as a group following dispersal. Consequently I have no quantitative data on rates of grunting in different social contexts by animals older than 1 year. Yearlings and older juveniles which were observed feeding at night vocalized rarely; this was markedly different from what was observed for hatchlings. Yearlings were heard grunting during emergence from the water to bask, when approaching or approached by an adult alligator, and when startled by my appearance. They also grunted while swimming with small groups of other yearlings; vocalizations in this context appeared to be used to maintain contact since these individuals answered each other's grunts.

One-year-old alligators were observed in the midst of many pods, and one yearling was captured twice with the same pod. Yearlings observed with pods of hatchlings were of normal size for their age. These yearlings emerged, basked, and foraged along with the hatchlings, but grunted infrequently during these activities.

Parental Care

The amount of parental care that pods received was extremely variable in nature and in duration. The shyness that most adult alligators in all habitats exhibited towards humans made direct observation difficult; for reasons discussed below I regard my assessments of the degree of parental care of different pods to be minimum estimates. With one exception (see below), only a single adult alligator was ever observed in close association with a pod of hatchlings. The only adult alligator at the Carr property was known to be a female; her behavior was consistent with the behaviors of other protective and attentive adults, and I follow McIlhenny (1935) in believing all such alligators to be female.

I used three artificial categorizations for female parental behavior in *A. mississippiensis*: minimal care, attendance, and defense. Pods that received minimal care included some with which females were sighted on one or two occasions, but most minimal care pods were never observed with an adult alligator. Females were considered attentive if they were present on at least one-third of all observations of the pod but did not threaten humans when the pod was approached. Defensive females were those which actively threatened me when I approached a pod and/or attempted to capture the young.

It appeared that most if not all pods in the study received some parental care. The appearance of all successful nests on Payne's Prairie and on Orange and Lochloosa lakes indicated that they were probably opened by the female (Deitz and Hines, in press) and the pods were probably then led or carried to the guard pool (Meyer, 1977). The role of the female parent in subsequently creating additional wallows and trails which determined movements of the pod has been discussed above. There were evidences of regular adult alligator presence (*i.e.*, trails, tracks, recent excavations, smashed vegetation) associated with most pods where I never actually observed adult alligators.

Approximately one-third (34%) of the pods encountered in this study were cared for by attentive or defensive females, although this composite figure was biased by differences in female behavior between locales (Table 4-1). The major difference between attentive females and all others observed was apparently their reduced shyness towards humans and/or boats. Eight attentive females were observed on 22 occasions. During 9 encounters (41%) females remained largely motionless while I observed the pod, and submerged only when I approached to within about 10 m. On 3 occasions (36%), females submerged immediately after my arrival. Two females (9%) initially moved toward their pods but submerged when I continued to approach, and on three additional encounters (14%) females responded by submerging, returning to within about 10 m, submerging, returning again, etc., for the duration of my visit. Postures and threats such as those used by defensive female alligators were not observed.

Defensive female alligators protected their pods with a series of threat displays directed towards me. If ignored, these displays

Table 4-1. Parental care of hatchling alligators.

Locale	Pods Observed	Type of Care			A or D
		Minimal	Attended	Defended	
Payne's Prairie	13	7	3	3	6 (46%)
Orange Lake	20	14	4	2	6 (30%)
Lake Griffin	11	10	1	0	1 (9%)
Lake Wauberg	5	5			0
Station Pond	2	2			0
Biven's Arm	4			3	3 (75%)
Carr property	3			3	3 (100%)
pond in south Gainesville	1		1		1
Total	59	39 (66%)	10 (17%)	10 (17%)	20 (34%)

culminated in approaches by the female which, if not actual attacks, were sufficiently menacing that I ended the encounters by retreating. I provoked 24 encounters with 9 different defensive alligators; two of these alligators were observed with pods in two separate nesting seasons.

Upon observing my approach (usually by wading) near their pods, defensive females swam toward me with their bodies inflated. This elevated their dorsal surfaces several cm above the surface of the water, and this posture was easily distinguished from the normal floating or swimming posture where the dorsum was but slightly emergent. Females normally halted 5 or 10 m away from me in the inflated or head-emergent tail-arched posture (Garrick *et al.*, 1978), and were at this point usually closer to me than any of the hatchlings were. If I continued to approach or remained stationary, from one to several loud hisses were emitted. Females were stationary as they emitted these hisses; the head was elevated out of the water and pointed toward me, the snout was lifted and the jaws were from slightly to widely agape. This posture was identical to the bellow-growl posture described by Garrick *et al.* (1978, Fig. 7A) although bellow-growls were not heard. One female thrashed her tail from side to side while hissing. If I attempted to move to one side, females oriented their heads to follow my movement and then repositioned their bodies. Subsequent behavior was variable. If I remained stationary, some females withdrew to their pods within several minutes, while others maintained the bellow-growl stance or head-emergent tail-arched posture and continued to hiss. Advances by me were met with renewed hissing and jaw gaping. During one nocturnal

encounter, a female bellowed twice at me from less than 5 m away. Females lunged at me twice with jaws opened wide; one of these animals then pursued me for approximately 10 m.

Although defensive females sometimes responded to my approach before any reaction by the pod was observed, distress calls by the hatchlings were clearly important in stimulating female protective behavior. I was sometimes able to approach and observe defended pods without being detected by the female. When these hatchling finally became alarmed by my movements and began grunting, the female appeared immediately. Females in these situations seemed initially to swim toward the vocalizing hatchlings and appeared to orient to me only after they reached the pod. On three occasions I captured hatchlings from defended pods; these hatchlings grunted continuously after capture. This provoked extremely rapid approaches by all three parents. In contrast to other encounters (which, except for the one pursuit described above, ended with my retreat from the vicinity of the pod), these females all pursued me as I retreated with hatchling in hand. Two of the females followed me out of the water up onto the bank, and the third pursued me for approximately 10 m through shallow marsh. After all three of these alligators had reached the limits of their pursuit, I returned and released the captive hatchling between us. In all three cases the hatchlings (which continued to vocalize) were ignored.

In addition to exhibiting threats toward humans, defensive female alligators were more consistently present with their pods than attentive females. Females were present at 38 of 39 visits (97.4%) to 6 defended

pods, but were observed on only 20 of 37 visits (54.1%) to 6 attended pods ($p < .01$, Chi-square test). The behavior and regularity of both attentive and defensive females with their pods was similar to their behavior at their nests during incubation (Table 4-2). All pods from nests that were undefended received minimal care. There were no evident differences in distance of pod movements, use of additional wallows, or timing of movements from nest to den between pods which received different degrees of protection against humans. There were also no significant differences in first-year mortality between attended or defended pods ($n = 3$, for pods with reliable data) and minimal care pods ($n = 20$), although sample sizes were quite small and these comparisons were made across different locales (see Chapter III).

Two adult alligators were observed with one Orange Lake pod on 6 May 1977 and again on 20 May 1977. The length of the larger of these adults was estimated at 3.0-3.4 m (10-11 feet); it was assumed to be a male on the basis of size (Joanen *et al.*, 1974) and behavior (Garrick *et al.*, 1978). Courtship was observed between these two adults on 6 May; I assumed but could not be certain that the male observed with the presumed female on 20 May (same location) was the same individual observed on 6 May. On both dates, hatchlings were ignored by the male and did not respond to his presence. The only reaction that I observed were sporadic grunts by some individuals in association with movements of the adult; some hatchlings moved slowly out of the path of the male as he swam past them.

The duration of parental care by attentive and defensive females was variable (Table 4-2). All attentive and defensive females appeared

Table 4-2. Behavior of adult female alligators observed at nests and with pods.
Behaviors: A = attentive, D = defensive. Numbers after behavior
are number of occasions on which female was present/total visits.

Year and Nest No.	Locale	Female Behavior		Last Day Observed
		At Nest	With Pod	
74CR2	PP	D, 19/20	D, 5/5	12 Oct. 74
75CD1	PP	A, 6/10	A, 5/10	24 Oct. 74 - ♀ absent in spring 75
76CD6	PP	A, 4/9	A, 4/8	5 Nov. 76 - ♀ absent in spring 77
75K1	PP	D, 5/10	D, 13/13	24 June 76
77K1	PP	D, 4/4	D, 2/2	
74	Carr	D, 28/28	D, 13/13	24 Oct. 74 - ♀ not defensive in spring 75
76	Carr	D, 2/2	D, 3/3	late Oct. 76 (Carr, pers. communication)
76	Newnan's Lake	(D)*	D, 3/3	

*D. Crider, pers. communication

to care for their pods from hatching to the onset of cold weather; analysis of the movements of minimal care pods suggested that they too had some association with the female throughout the first two months following hatching. Some females remained in close association with their pods through the following spring, while others clearly did not (Table 4-2). The latest date that maternal pod defense was observed was 24 June 1977. The defending female on this occasion inflated her body and swam directly at me as I approached--a response consistent with my other encounters with this female. One pod on Orange Lake (not shown in Table 4-2) was regularly attended through 20 May of the year following hatching.

Pod attendance or defense also varied with locale (Table 4-1). Differences in the extent of human disturbance (and possibly, therefore, harassment of alligators by humans) between these locales seemed the most likely explanation for this. Payne's Prairie had been a state preserve and closed to the public since 1971; furthermore, long-time residents of the area agreed that during private ownership of the Prairie trespassers were probably more often molested than alligators. Orange Lake, Lake Griffin and Lake Wauberg were all regularly used by fishermen and hunters. However, there were large portions of Orange Lake that were normally inaccessible to most boats; this was not the case on Lake Griffin or Lake Wauberg. Human-alligator contact on Station Pond was presumably minimal, but too few pods were observed for valid comparisons. Biven's Arm, the pond in south Gainesville (both within the Gainesville city limits), and the Carr property were localities at which alligators frequently encountered humans but were

not exposed to motorboats and probably received little harassment. Most of the pods in these three areas were attended or defended (Table 4-1). Although sample sizes were small, there was no indication that duration of pod attendance was correlated with habitat. As discussed above (Chapter III), dispersal of pods began at about the same time in all areas.

Discussion

The activity cycle of wild *Alligator mississippiensis* appears to be typical of that reported in studies of thermoregulatory behaviors of other crocodilians. Synchronous emergence from the water to bask has previously been reported for both adult and juvenile *A. mississippiensis* (Lang, 1975a, 1976) and *Crocodylus niloticus* (Cott, 1961; Modha, 1968). After basking, a return to the water for the remainder of the day with occasional brief re-emergences is also characteristic of other crocodilians studied (Cott, 1961; Modha, 1968; Lang, 1975a; Johnson, 1973). Two to four-year old *A. mississippiensis* in outdoor pens in Florida studied by Lang (1976) emerged at sunrise and remained on land until sunset; my observations of wild juveniles of this age suggest that later emergences in the morning as well as an earlier return to the water are typical under normal conditions.

Social coordination in the timing of emergence from cover and movement to land has not been previously reported for any crocodilian. The most striking consequence of the rapid peak in vocalizations as juvenile *A. mississippiensis* emerged from cover and moved to a common basking site was the close aggregation of pod members. Similar behavior

may occur in *Crocodylus niloticus*, based on the observations of Modha (1967, p. 94) that hatchlings of this species basked in clumps with "four or five animals sitting on top of one another." While some reaggregation occurred in the early morning hours following a night's feeding, pod members were still scattered at sunrise, and some individuals were 10 m or more from the main group (see Fig. 4-8). The morning vocalizations produced a sustained signal which probably enabled most stragglers to locate the main group. Diel basking rhythms have been reported for juvenile *A. mississippiensis* (Lang, 1976) and *C. niloticus*; there is no reason why isolated juveniles could not predict the approximate timing of these vocal peaks and be prepared to orient to the group when they were heard. Isolated animals could generate additional vocal cues, if needed, by grunting and orienting toward the subsequent vocal responses.

The similarities between the re-aggregations following disturbance of the pod and the social bask also suggested that these choruses of grunts helped to achieve pod cohesion. Individuals vocalizing as they emerged from cover were likely to be answered by other nearby juveniles. Moving individuals were likely to continue vocalizing even if unanswered. The most likely orientation of individual alligators responding to the grunts of others would therefore be toward the largest concentration of juveniles. Pitman (1936, in Cott, 1961) referred to increases in vocalizations by hatchling *Crocodylus niloticus* as they regrouped after disturbances.

The rise in VAH associated with evening emergence may also promote pod cohesion, although a rapid dispersal of feeding individuals

followed immediately. Based on the hypothesis that juvenile grunts functioned as a contact call, Campbell (1973) predicted that rates of vocalization by a pod would increase after sunset when visual cues became useless. This was partly true for *A. mississippiensis*; VAH did remain elevated for at least one hour after sunset. Thereafter, vocalizations declined along with feeding and other movements by the pod, and the return to cover prior to sunrise took place with little grunting by moving juveniles. Vocalizations may serve to limit evening dispersal in so far as feeding juveniles may attempt to remain in audible range of other juveniles. However, studies of orientation and homing in juvenile *A. mississippiensis* indicate that celestial cues may also be used to return successfully (P. Murphy, 1978; G. Rodda, unpublished data).

Contexts in which juvenile *A. mississippiensis* grunted were discussed briefly by Herzog (1974). His observations and mine are in agreement with respect to the association of movement with grunting in all contexts, and support the hypothesis that grunting promotes pod cohesion by acting as a contact call. My observations of hatchlings separated from a pod suggest that vocalizations alone provide sufficient information for accurate relocation of the main group. The increase in calling observed in isolated alligators have also been observed in gallinaceous birds isolated from their mates (Potash, 1975). The broad range of frequencies used may facilitate location of the caller in the densely-vegetated habitats often occupied.

In addition to serving as a contact call, the juvenile grunt also seems to alert other hatchlings to unusual or new stimuli, without conveying any information about their nature. Campbell (1973), Herzog

(1974) and I have all observed grunting during feeding; it appears that these calls might stimulate other juveniles to forage as well. Movements (including arrivals and departures) of the female stimulate grunting, and hatchlings are attracted to the female's location by the grunting of other juveniles near her if she is invisible to them. The female's continued presence thus also insures group cohesion. McIlhenny (1935) reports a female *A. mississippiensis* calling young to her from the nest, and H. Hunt (unpublished data) has regularly observed deep grunts (Garrick *et al.*, 1978) used by female alligators to attract their pods. Similar behavior has been reported at hatching in *Caiman crocodilus* (Alvarez del Toro, 1969). I never heard deep grunting by female *A. mississippiensis* in attendance with their pods; it may be that the deep grunt is frequently used only when pods are being transported or attracted to a new location.

My observations of the juvenile distress call support Campbell (1973), who has suggested that this call serves only an alerting function and does not necessarily communicate alarm to other juveniles (see Chapter V). Hatchlings and other juveniles are consistently attracted to the calls of captive siblings; in my experience juveniles appear frightened and seek cover only if alarming visual stimuli (*i.e.*, close approach by large objects such as humans or boats) are also present when distress calls are given.

The group behaviors of hatchling *Iguana iguana* show interesting similarities to those of young *A. mississippiensis*. Hatchling iguanas emerge from nest holes in groups, and hatchlings from several different holes have been observed to emerge simultaneously (Burghardt *et al.*,

1977). Young iguanas remain in small groups after leaving the nest, and show some social attraction in selecting common basking and sleeping sites. Visual cues appear to be the mechanism by which contact is maintained, and the conspicuous dark eyespot of young iguanas has been likened to the contact calls of vocal species (Burghardt, 1977). The increased predator detection resulting from these groups is probably their principal adaptive value (Greene *et al.*, 1978).

The frequency and duration of parental care in Florida *A. mississippiensis* are both much greater than has been stated by some authors (Neill, 1971); my observations basically support McIlhenny's (1935) generalizations. The duration of pod defense through June of the year after hatching indicates that at least some female *A. mississippiensis* are involved with nesting and care of the young virtually all year. This suggests one explanation for the restricted movements of adult female *A. mississippiensis* when compared with movements of males (Joanen and McNease, 1970, 1972a; Goodwin, 1977). The dispersal of pods beginning in June may be related to the initiation of nesting by females at this time. Some females devote considerable time to nest construction and during incubation may seldom leave the nest site (Carr, 1976; Deitz and Hines, in press). Parental care of the previous year's young must certainly be reduced once these activities have begun.

The restricted dispersal of young *A. mississippiensis* during their first summer could permit them to receive some maternal care, although its extent is probably limited by the female's preoccupation with nesting. Juveniles presumed to be 2 years old have been observed with

females during droughts (Fogarty, 1974; Chabreck, 1965), and similar associations are reported for *Caiman crocodilus* (Staton and Dixon, 1977). Juvenile *A. mississippiensis* greater than 1 m TL were rarely observed near hatchlings and in view of their evident attraction to juvenile grunts and persistent references to cannibalism in the crocodilian literature, it seems possible that they are actively excluded by protective females. A 1.2 m alligator was seen to enter an enclosure containing hatchlings and eat one (D. Crider, pers. communication), and I saw an adult female threaten and chase a subadult during her response to playbacks of juvenile grunts (see Chapter V). Hunt (1978) has several observations of the exclusion of captive juvenile *Crocodylus moreletii* from groups of hatchlings by the parent female.

The sequence of defensive behaviors used by females with their pods includes several postures which are also used in intraspecific agonistic encounters: the inflated posture, the head-emergent tail-arched posture and the bellow-growl posture (Garrick *et al.*, 1978). The graded series of threats which I observed in pod defense is similar to that which Kushlan and Kushlan (in press) and I have observed in females defending their nests. In both pod and nest defense, females followed initial approaches with open-mouth threat postures, hissing, and open-mouth lunges. I did not pursue the pod defense sequence beyond open-mouth lunges and subsequent pursuit by the female, but Kushlan and Kushlan (in press) have shown that females will deliver "mock bites" before actually biting dummy nest intruders. In view of the similarities, the same may occur during pod defense. One important difference in the two series of behaviors is the orientation of the

female. Alligators defending nests are clearly oriented to the nest; they move directly toward it when approached and often display while lying across it (Kushlan and Kushlan, in press; personal observations). Female alligators responding to my approach of their pods initially moved toward the pod (this may have been a response to the vocalizations of the young), but thereafter directed all threats toward me.

While defensive female *A. mississippiensis* approached me prior to any reaction by their young, distress calls by juveniles augmented the intensity and persistence of female threats; McIlhenny (1935) and Kushlan (1973) have made similar observations. The fact that some females appeared only after hatchlings began to emit distress calls suggests that this call may convey alarm to adults, or at least alert them of novel stimuli. H. Hunt (unpublished data) has observed a blind female *A. mississippiensis* which nested successfully and cared for her young by responding vigorously to their calls.

Female *A. mississippiensis* which protect their young against humans presumably protect them against other predators. I did not observe any instances of this, although the defensive female at the Carr property has been observed to drive away Great Blue Herons, *Ardea herodias*, which attempted to eat hatchlings (A. Carr, pers. communication). Defensive behavior by nesting female *A. mississippiensis* significantly reduces nest predation (Metzen, 1977; Deitz and Hines, in press), and one would therefore expect defensive behavior to be negatively correlated with pod mortality. It was not. This could be attributed to small sample sizes, but a more important failure in this study involved my inability to observe many females with their pods. These pods were

classified as minimal care pods, but they clearly had an adult alligator in attendance at least part of the time, and may have received substantial protection against predators.

Female *A. mississippiensis* which did not defend their nests against humans did nevertheless visit and maintain them, and one nesting female which had never threatened humans was observed to drive off a raccoon, *Procyon lotor* (a known nest predator--Deitz and Hines, in press). Learned avoidance of humans may not necessarily disrupt all reproductive and parental activities of alligators, even though the parental care of alligators in areas with high human activity was probably somewhat reduced. Both Reese (1915) and McIlhenny (1935) believed that human disturbance affected the protective behavior of female *A. mississippiensis*.

The behavior of other juvenile crocodilians has not been well-studied, although scattered accounts suggest that it may be similar to that of *A. mississippiensis*. The young of all crocodilians vocalize (Neill, 1971; Campbell, 1973; Herzog and Burghardt, 1977). Pods which are defended by a parent are known to occur in *Crocodylus niloticus* (Cott, 1961, 1971; Modha, 1967), *Crocodylus palustris* (Dharmakumarsinhji, 1947), *Crocodylus acutus* (Alvarez del Toro, 1974), *Crocodylus moreleti* (Alvarez del Toro, 1974) and *Caiman crocodilus* (Staton and Dixon, 1977). Medem (1971) indicates that female *Melanosuchus niger* and *Paleosuchus palpebrosus* both defend nests, but that only the young of *M. niger* are gregarious and are defended. Little information is available beyond the fact that pods occur and are defended. Both Cott (1971) and Modha (1967) have observed hatchling *Crocodylus niloticus* basking on the head and back of adults; Modha (1967) also reports increased vocalizations by groups in response to the arrival of the mother. Cott

(1961) indicates that juvenile *C. niloticus* are extremely cryptic by day and are presumably hiding in dense vegetation. Lang (1975b) reports that hatchling *Crocodylus acutus* in Florida remain under cover by day and emerge at night, and Webb *et al.* (1977) have described tidal influences on the behavior of hatchling *Crocodylus porosus*, an estuarine species. Flight and cover-seeking behaviors are reported in response to vocalizations of other hatchlings in wild *Crocodylus niloticus* (Pooley and Gans, 1976), and *Caiman crocodilus* (Campbell, 1973).

Response to vocalizations and care of the young by adult males has been observed in captive *Crocodylus niloticus* (Pooley, 1977), *Crocodylus moreletii* (Hunt, 1975) and *Caiman crocodilus* (Alvarez del Toro, 1969, 1974). In the wild, males do not seem to be involved in parental care in *Crocodylus niloticus* (Cott, 1961, 1971; Modha, 1967) or *Caiman crocodilus* (Staton and Dixon, 1977). While males are evidently capable of caring for young in these species, their normal contribution to parental care may be negligible. Webb *et al.* (1977) present evidence suggesting that the movements of *Crocodylus porosus* are similar to *A. mississippiensis*, in that adult females may have restricted home ranges near breeding areas while males travel extensively (Webb and Messel, 1978). Such differences in movement patterns would imply that most, if not all, parental care is likely to be maternal.

Duration of parental care is likewise uncertain for most species of crocodilians. Cott (1961) has observed maternal defense 81 days after hatching in *Crocodylus niloticus*, with other observations of shorter duration, and defense has been observed 5 weeks after hatching in *Crocodylus acutus* by Alvarez del Toro (1974). Attendance of the pod without active defense occurs for at least 4 months in some female

Caiman crocodilus (Staton and Dixon, 1977) and at least 2 months in some *Crocodylus porosus* (Webb *et al.*, 1977). All of these studies also suggest that there is considerable individual variation in the duration and expression of parental care.

CHAPTER V
EXPERIMENTAL ANALYSIS OF THE VOCALIZATIONS
OF JUVENILE ALLIGATORS

Introduction

The vocalizations of crocodilians have long been known to scientists; some of the oldest accounts include references to bellowing or roaring by adults as well as grunting or chirping by the young (see reviews by Cott, 1961, 1971, and Neill, 1971). Three main functions have been attributed to these juvenile vocalizations: attraction of the parent at hatching time to release the young from the nest, attraction of the parent or other adults for aid in distress contexts, and attraction of siblings and other juveniles to maintain group cohesion. Data at present available (many of them from captive studies) have supported some or all of these speculations for 11 of the 21 extant crocodilian species, and it is probable that parental care is elicited in these contexts by vocalizations of all 21 species (see Chapter IV). Lee (1968) has suggested that vocalizations of *Alligator mississippiensis* might help synchronize developmental rates late in the incubation period and thus insure a synchronous hatch. Data from his single experimental test support his hypothesis, but the experiment has never been repeated (Lee, 1968). The possibility that juvenile vocalizations might function as alarm calls within sibling aggregations has also been discussed (Staton, 1978).

Few experimenters have examined further the function of juvenile vocalization. Playbacks of recordings of conspecific juvenile grunts were used successfully to stimulate nest opening by captive female *Crocodylus moreletii* (Hunt, 1975) and *C. niloticus* under semi-natural conditions (Pooley, 1977). Both of these investigations also reported approaches to playbacks of juvenile grunts by adults of both sexes; additional parental behaviors were then elicited by the presentation of eggs and/or hatchlings (Hunt, 1975; Pooley, 1977). Captive adult *C. palustris* attacked keepers when tape recordings of juvenile calls were played (Whitaker, 1974). Captive adult and subadult *A. mississippiensis* also approached playbacks of hatchling calls (Herzog, 1974). Campbell (1973) reported that captive juvenile *A. mississippiensis* vocalized and approached the speaker in response to playbacks of their calls (and a variety of other sounds also), but in similar experiments with *A. mississippiensis* Herzog (1974) found no consistent response. Groups of hatchling *C. niloticus* vocalized and moved toward playbacks of their calls conducted by Pooley (1977).

Observations of parental defense of young *A. mississippiensis* by McIlhenny (1935), Kushlan (1973) and me (Chapter IV) all indicated that vocalizations by the juveniles were important in provoking approaches and other protective behaviors by adults. My major objectives in conducting playbacks to adult alligators were to characterize more completely the responses of adult and subadult alligators of both sexes to juvenile vocalizations, and to test the hypothesis that juvenile vocalizations alone were sufficient to elicit protective behavior by parent females. Juveniles observed during the study vocalized in a variety of contexts

(Chapter IV); my main purpose in conducting both field and tank playbacks to pods of hatchlings and other juveniles was to characterize group and individual responses to vocalizations in the absence of other specific stimuli.

Field observations of the grunts of juvenile *A. mississippiensis* and their use in natural settings supported Campbell's (1973) contention that the juvenile distress call was distinguishable from some other juvenile grunts only by the context in which the calls were given (see Chapter IV). However, juvenile *A. mississippiensis* did vocalize more rapidly when alarmed (*i.e.*, the repetition rate for grunts given by one individual increased). It therefore seemed reasonable to test the hypothesis that this increased rate of vocalization might indicate a distress context by conducting playbacks of grunts with different repetition rates.

Methods

Field Playback Experiments

Tape loops of hatchling and yearling calls were made from calls recorded in an acoustically insulated room using an AKG 451E microphone and Nagra III or Tanberg Model 11 tape recorders at a tape speed of 9.5 cm/sec. Tape loop 1 was prepared from the "distress" calls of a hand-held hatchling alligator (SVL 12 cm) and loop 2 was prepared in an identical fashion from calls of a 26.5 cm (SVL) juvenile. In order to examine the effects of call rate on behavior, loop 1 (repetition rate approximately 1 call/sec) was used to produce loop 3 (repetition rate

0.25 calls/sec). Several hatchlings calling together were used to produce a recording of multiple vocalizations (loop 4). On the basis of spectral qualities and context (the alligators were forcibly restrained and sometimes pinched to induce calling), all of these recordings fit definitions of "distress" calls by Neill (1971) and Burghardt and Herzog (1977). The recorded calls of an adult male *Rana grylio* used as a control were obtained from Master 13b, Bioacoustic Archive, Florida State Museum.

Equipment for most playbacks consisted of one 8-inch acoustic suspension speaker connected with a 10 m extension cord to a Roberts 6000 stereo tape recorder. The output of this system in dB SPL for different tape loops at the playback volume settings used was calibrated using a 2.5 cm B & K condenser microphone placed 200 cm from the speaker in an acoustically insulated room (Insect Attractants Laboratory, USDA, Gainesville, FL) and connected to a B & K 2608 measuring amplifier. Amplitudes of the distress calls of two hatchling alligators also measured in this fashion ranged from 50 to 64 dB SPL; most field playbacks were conducted at 58-59 dB SPL at 200 cm. The volume of field playbacks conducted with other systems was not measured, but was set at levels I regarded as normal.

Field playbacks were conducted in a variety of situations. Speaker placement was at water level on a float, on land adjacent to water, or in the bow of a boat. I remained as far from the speaker as was practical for observing responding alligators with binoculars. Many playbacks to adults were made after the alligator had already

been sighted (usually basking); such alligators were almost certainly aware of my presence. In other instances, particularly playbacks to juveniles, natural cover was used effectively for concealment, and alligators in these situations were probably unaware of my presence. Some playbacks were conducted with a juvenile alligator tethered near the speaker with a light string around one hind foot. The tether permitted the juvenile to assume normal postures, but forced it to remain within 150 cm of the speaker.

Playbacks were presented for at least 5 minutes. A positive response was scored if an alligator moved steadily toward the speaker for at least two body lengths. Negative responses were scored if movement was directed sideways or away from the speaker. For animals initially visible, response latency was the time from start of the playback to the beginning of a directed movement. Response latency for other alligators was the time from the start of the playback to the time of their appearance; thus, mean response latencies calculated were biased in favor of larger latencies.

Tank Experiments

Controlled experiments on the response of juvenile alligators to recorded calls were carried out in 1977 at the Savannah River Ecology Laboratory in Aiken, South Carolina, using the apparatus described by P. Murphy (1978). This consisted of a circular tank (swimming pool) 305 cm in diameter and 91 cm high, filled to within 20 cm of the top. Opaque, uniformly dark-colored cloth screens were placed around the perimeter of the tank, and observations made through slits in the screens.

This left celestial cues and irregularities in the screen and tank as the only visual cues available to experimental alligators. The playback apparatus consisted of two 8-inch acoustic suspension speakers connected to a Roberts 6000 stereo tape recorder. The speakers were placed in 180° opposition just outside the screen, either NS-SE or NE-SW. Air temperatures at the time of testing were 26°C-33.5°C during the day and 25°C-27°C at night. These temperature ranges corresponded to those measured when juveniles were active in the field. All tests were run under clear, moonless skies.

Tests were conducted both day and night. Alligators were introduced into the tank from the sides of the pool; different release points were used for each trial. A release device located in the center of the tank was used during preliminary trials, but abandoned because it appeared to interfere with the response of alligators to the playbacks. Following introduction, the test alligator was allowed two minutes to acclimate to the tank. After two minutes, the speaker farthest from the alligator, designated speaker A, was turned on. An "A" response was recorded if the alligator moved to the wall adjacent to speaker A (within 50 cm of the wall for hatchlings, 100 cm for yearlings). Once an A response was obtained, the other speaker (B) was turned on and speaker A was turned off. If the alligator then moved to speaker B, a "B" response was recorded and the experiment was terminated; otherwise speaker B or speaker A (depending on the response of the alligator) remained on for four minutes after initial presentation of the stimulus. Controls were observed for four minutes following the initial two minute acclimation period. Loop 1 was used for presentations of hatchling calls and loop 2 for yearling calls.

Results

Field Playback Experiments

Almost all subadult and adult *Alligator mississippiensis* of both sexes responded positively to playbacks of loop 1, the juvenile grunt (Table 5-1). Response latencies could not be determined for some responding alligators which were able to approach the speaker unseen and whose presence was then belatedly noted.

The slightly lower percentage of positive male responses versus positive female responses was not statistically significant and was possibly due to the fact that I was visible to all three non-responding males. However, there were other consistent sexual differences in response to playbacks of loop 1. Female response latencies were significantly lower than those of males ($p < .05$, t-test); although problems with visibility make these latency data somewhat suspect, males never exhibited the immediate orientation to the speaker that I observed with most females. In 11 of 12 instances, responding females assumed the inflated posture (Chapter IV) while swimming toward the speaker and/or while motionless during the playbacks; only 2 of 7 males used this inflated posture when responding to playbacks (difference significant, $p = .01$, Fisher exact probability test). All alligators returned to a normal floating posture after playbacks ceased. They usually remained motionless for a few minutes, then swam back in the direction from which they had come. On two occasions I re-started the playback after alligators had begun to swim away; both alligators (adult females) returned to the inflated posture immediately and oriented toward the

Table 5-1. Responses of adult and subadult American alligators to playbacks of the juvenile distress call.

Alligators Tested	No. of Animals	No. of Trials	No. of Positive Responses	Maximum Response Latency (min) $\bar{X} \pm \text{s.d. (range)}$
Ad. ♂	8	10	7	6.0 (4.0-9.3) n = 3
Ad. ♀	7	12	12	1.2 $\pm$ 1.1 (.1-3.5) n = 9
Unk. Ad.	5	5	5	9.0 $\pm$ 6.2 (2-16) n = 4
Subadult	5	5	5	0.7 $\pm$ 1.3 (.1-3) n = 5
Total	25	32	29 (91%)	

speaker. Females also came closer to the speaker before stopping than males, although this was not statistically significant; 7 of 12 females stopped 2 m or less from the speaker, while only 2 of 7 males approached this closely. On one occasion in which a truck was used as a blind and the speaker placed next to it on a levee, a male and female alligator both emerged from an adjacent canal and climbed up the levee in response to a playback.

Three of the above playbacks of loop 1 to females were conducted with a juvenile alligator tethered next to the speaker. The first of these was conducted on 15 May 1977 at the Carr pond to a female which had nested successfully the previous year. The speaker was placed on floating water weeds (mostly *Hydrocotyle umbellata*) approximately 3 m from the north shore of the pond, and the juvenile (TL 35 cm) tethered to adjacent vegetation. I observed from bushes approximately 15 m to the northwest of the speaker; all locations (letters) in the following account from my field notes refer to Fig. 5-1.

1632 - Playback begun.

1633 - Adult female alligator (total length approximately 2.6 m) observed at A (Fig. 5-1) swimming toward the speaker in an inflated posture. Immediately after becoming visible, the female turned toward a 1.2 m subadult alligator (not previously observed) at B and swam rapidly toward this juvenile, chasing it into the marsh to the southwest. The female (still in the inflated posture) stopped at B for approximately 15 sec.

Figure 5-1. Response of an adult female alligator at the Carr property to playbacks of juvenile grunts and to a hatchling alligator tethered near the speaker. Letters refer to locations described in the text.

- 1637 - Female resumed swimming toward speaker.
- 1640 - The female arrived at C. She had maintained the inflated posture for the entire trip, but deflated as she arrived and paused briefly. The female then pushed her head into the weeds toward the speaker, and at this time the tethered juvenile began to grunt rapidly.
- 1641 - The female submerged her head with a quick downward and slightly backward movement, and immediately surfaced it.
- 1641:45 - The head submergence was repeated, and the juvenile ceased grunting.
- 1642:45 - The female pushed her head forward (north) into the weeds next to the juvenile and again briefly submerged her head.
- 1643 - The female bit quickly to the side into the weeds by the juvenile, then pulled her head back and submerged completely. She surfaced at D, still facing the speaker, and assumed the inflated posture; masses of weeds were sticking out of both sides of her mouth.
- 1643:45 - The female shook her head from side to side once and deflated.
- 1645 - The female moved her head slightly, and the previously tethered juvenile became visible next to her snout. She had apparently carried the juvenile (along with adjacent plants) from the speaker to D in her mouth.
- 1646 - The juvenile began swimming slowly toward the speaker.
- 1647:30 - Playback was turned off. The juvenile was approximately 1.5 m from the female's snout.

1648 - The female turned and began swimming south. The juvenile was still tethered to the vegetation stuck in the female's jaws and was pulled underwater backwards as the female moved. The juvenile vocalized as it submerged, and the female then stopped swimming.

1650 - The juvenile surfaced next to the female's head. A second smaller alligator (size consistent with 1976 hatchlings) was observed at H, oriented toward the female.

For the next 20 minutes, the female alternated short (5 m or less) movements to the south in a normal swimming posture with return movements toward the speaker (which was turned off) in the inflated posture. These returns were initially associated with the grunts of the juvenile as it was pulled under by the tether stuck in her jaws, but continued in the absence of any discernable stimuli after the female released the remaining weeds from her jaws at 1703. Once released, the juvenile continued to orient to the female's head. It crawled up on her neck twice and on the second occasion actually rode there as the female moved about 2 m.

A playback with a tethered juvenile alligator was repeated with the Carr female on 4 June 1977. This female had begun nest construction and approached from the vicinity of her nest site in response to the playback. The tethered juvenile on this occasion did not vocalize or move after the female's arrival at the speaker, and it may have been invisible to her in the weeds. The female remained near the speaker for 5 minutes before swimming into the marsh near her nest.

Three other playbacks of loop 1 with tethered juveniles were attempted on Orange Lake in areas previously known to contain females

with young (sighted in the area within 2 weeks of the playback). None produced a response. However, no adult alligators were sighted in the playback areas on the dates of the playbacks; consequently no conclusions could be drawn from these failures.

At 1430 on 15 September 1977 a playback of loop 1 with a tethered hatchling (TL 28 cm) nearby was presented to an adult female alligator (TL approximately 2.4 m) on Biven's Arm. This female had nested successfully in 1977 and had previously defended her nest and pod against humans (D. Jackson, personal communication). The female responded immediately to the playback by moving up to the speaker with her head near the hatchling, and appeared to orient alternately over the next 10 minutes between the speaker, the tethered hatchling, hatchlings from her pod which had followed her and were also vocalizing, and my movements as I attempted to film her behavior. Approximately 10 minutes after the start of the playback one of her head movements brought her eye next to the tethered hatchling, which was grunting rapidly at this time. In one continuous movement the female swung her head toward the hatchling, tilting her snout down slightly as she did so, opened her mouth and closed it around the tethered hatchling. She remained in this position for approximately 10 seconds, then opened her mouth and released the hatchling as she backed away about 60 cm. These movements were not sufficient to pull the hatchling off its tether; it continued to struggle and call occasionally after being released. By this time at least 7 other hatchlings from the pod had followed the female and approached to within 2 m of her. One of these hatchlings climbed on the female's snout while she was facing the tethered hatchling and the

speaker (which was turned off). The female responded by lifting the tip of her snout out of the water and then tilting her snout (by rotating her head around its long axis) approximately 20 degrees to the left; the hatchling slid off after the third tilt. This was the only occasion on which I observed a hatchling shaken off a parent female's head or body. The female and her pod remained by the speaker and the tethered hatchling until after sunset (2200). I removed the tethered hatchling on the next day; it was uninjured.

The responses of groups of hatchlings to field playbacks of loop 1 were quite variable; the proportion of individuals in a pod responding to a playback ranged from 0 to 100%, making generalizations difficult. The "typical" response of individuals in a pod was bimodal: there was an initial positive response and approach to the speaker, followed by a pause and then a steady movement away from or oblique to the speaker into vegetation. For 10 pods, a mean of $31.0 \pm 31.0\%$ of the hatchlings visible responded positively to the playback; this was significantly more than the $11.9 \pm 16.8\%$ which initially responded negatively ($p < .01$, Chi-square test). Playbacks of *Rana grylio* calls presented in identical fashion to 3 groups of hatchlings and 2 individual one-year old alligators produced no reaction.

Many positively-responding hatchlings emerged from cover where they had not been visible prior to the start of a playback. The average increase in number of hatchlings visible during the playback was $40.7 \pm 47.3\%$ (range 0-150%) for 9 playbacks, and this increase was significant ($p < .01$, t-test for paired samples). However, by the conclusion of the playback the mean increase in number of juveniles visible was an insignificant $2.5 \pm 42.9\%$ (range -100 to +57%); this was

a reflection of the movement into cover by many animals which had initially responded positively. There was also a slight, non-significant increase in the proportion of the pod in the water for 5 playbacks.

Hatchlings moving toward the speaker or cover grunted, as was customary for moving animals. Other pod members occasionally grunted in response to the speaker; these grunts appeared similar to those of group members in response to the grunts of solitary juveniles. The group as a whole did not appear to vocalize more during playbacks, and VAH's calculated for two playbacks were within normal ranges.

One-year old juvenile alligators responded similarly to loop 1 playbacks. Positive responses were obtained from 3 yearlings in one playback to a pod of at least 7 one-year olds, but 2 of these 3 then moved under cover after approaching the speaker. The third yearling had initially approached the speaker and paused. It then turned 90 degrees to its right and began swimming rapidly towards an adult alligator (TL 2.4 m) which was approaching the speaker in the inflated posture from about 15 m away. The yearling entered a clump of vegetation directly in the path of the adult and was lost from view. Five of 7 individual yearlings observed with pods of hatchlings responded positively to playbacks of loop 1.

Three playbacks of loop 2 also produced bimodal responses from juvenile alligators. Positive responses were recorded from 5 to 8 hatchlings (68%), 6 of 8 yearlings (75%) and 2 of 2 subadults (summary of 3 playbacks); five of these yearlings and both subadults subsequently moved away into cover after this initial positive orientation. All three of these playbacks were conducted in locations where adult females were believed to be present, but no adults were seen. One 2.1 m adult

of unknown sex approached a playback of loop 2 in a normal swimming posture before it also turned and moved away.

Three additional field experiments were conducted in which playbacks with different call rates were presented successively to the same pod of hatchlings (Table 5-2). Loop 3 (which was created by spacing out the calls on loop 1) produced no response. Playbacks of loop 1 produced responses typical of other playbacks of this loop (see above): there was an initial positive response by several hatchlings (none of which had responded to loop 3), an increased number of animals became visible and finally there was a general movement away from the speaker into cover.

The responses of 2 pods to loop 4 were similar to those produced by loop 1, but more animals became visible and more responded positively during loop 4 playbacks (Table 5-2). Qualitative differences in the responses to loop 4 were especially striking. The response latency for all animals that responded positively was virtually 0, and most animals grunted. Hatchlings swam toward the speaker rapidly, and when stationary lifted their heads high out of the water while craning their necks up and forward, as though looking for the source of the commotion. Occasional head-lifting was observed during loop 1 playbacks, but not to this extent. Most hatchlings responding positively to loop 4 playbacks paused for 1.5-2 minutes after their initial approach, then turned away and swam slowly back under cover; they did not appear alarmed. An adult alligator emerged from shoreline vegetation near the pod during one playback of loop 4 and stopped, facing the speaker with head only emergent. This was the only occasion that an adult was observed with this pod.

Table 5-2. Responses of pods of hatchling alligators to juvenile grunts with different repetition rates.

Pod	Loop 3 0.25 calls/sec.			Loop 1 1 call/sec.			Loop 4 > 5 calls/sec.		
	Start	During	No. Pos Resp	Start	During	No. Pos Resp	Start	During	No. Pos Resp
1	5	5	0				5	7	6 (86%)
2	9	9	0	10	10	6 (60%)			
3	6	6	0	7	9	2 (29%)	6	10	5 (50%)

Tank Experiments

When tested individually in the arena at the Savannah River Plant, most hatchling *A. mississippiensis* oriented and moved to playbacks of hatchling distress calls presented at 1 call/sec (Table 5-3). Eight of the 11 hatchlings responding reversed an initial directional response in order to approach the playback (B response). Four of these animals grunted during responses, and two of these attempted to climb over the wall of the pool closest to the speaker. Controls were tested in silence (natural sounds available around the outdoor arena); these alligators swam slowly around the arena generally close to the wall of the pool, with frequent pauses and no preferences for a particular direction. Two controls vocalized. During the initial 2 minute acclimation period, the behavior of hatchlings which demonstrated A or B responses during testing was identical to that of controls.

Nine one-year old alligators were also tested in the arena using playbacks of yearling distress calls (loop 2). Results were similar to those obtained in hatchling tests: five yearlings produced B responses and the remaining 4 gave A responses. Five of these yearlings vocalized during testing. Only two controls were run; both of these animals remained largely motionless for most of the test period and did not vocalize.

Discussion

The results of field playbacks clearly indicate that juvenile vocalizations alone are sufficient to elicit some interspecific agonistic displays (inflated posture) and to provoke approaches by adult *A.*

Table 5-3. Response of hatchling alligators in an artificial enclosure to playbacks of juvenile grunts at 1 call/sec. All control animals swam slowly around the edge of the tank, pausing frequently.

	Number Tested	Experimental Response			Number Tested	Control Response
		A	B	No Response		
Day	9	2	4	3	6	Circled arena slowly
Night	7	1	4	2	7	Circled arena slowly
Total	16	3	8	5	13	

mississippiensis of both sexes. The differences in responsiveness between males and females further indicate that males are not principally involved in parental care in *A. mississippiensis*, although the possibility that males might be protective in some situations remains.

The responses of females to tethered hatchlings raise intriguing possibilities. Mouth transport of a juvenile in May, 8 months after the hatching season, clearly indicates that this is a well-developed protective response which is not necessarily restricted to hatching. It provides additional evidence that parental care in *A. mississippiensis* includes active protection of young up through the following nesting season. While protective females correctly oriented to playbacks and approached to within 1 m of tethered hatchlings, it appears that visual stimuli might also be necessary to induce mouth transport. Both females in which this was observed picked up juveniles only when these juveniles were visibly active near the speaker. Hatchlings which I released near protective females in attempts to duplicate Kushlan's (1973) observations all swam or crawled away normally and were ignored. The observation at Biven's Arm is particularly noteworthy, since the female in this instance chose to mouth the tethered hatchling, which was struggling, in preference to other young from her pod which were vocalizing nearby but swimming normally. The curious head submergences which the Carr female exhibited when next to the tethered hatchling have not been previously reported. They might have been associated with vocalizations, but if so these were inaudible to me 15 m away. The purpose of the head movements might be to signify presence of the adult to the juvenile.

An extremely active protective role for some female *A. mississippiensis* is suggested by my observations of mouth transport and those of Kushlan (1973). The female at the Carr property swam across the pond and probably left the remainder of her pod in response to a playback. In another trial, two adult alligators on Payne's Prairie climbed out of the water and up on to a levee, and J. Kushlan, M. Kushlan, and I (unpub. observations) have observed a female *A. mississippiensis* in the Everglades emerge from a canal and approach a truck where some of her hatchlings were being tagged. Positive responses to playbacks conducted while I was concealed from view were exhibited by 4 adult alligators (believed to be females) apparently associated with pods with which I had never seen an adult. These results further support the hypothesis (advanced in Chapter IV) that human presence may inhibit the behavior of females which are otherwise protective of their young.

The positive responses of subadult and adult male alligators to juvenile calls can be interpreted as weak evidence for protective behavior, general curiosity or investigation of cures which might potentially lead to food. Adult bullfrogs, *Rana catesbeiana*, are attracted to the distress calls of immature frogs and evidently make feeding attempts on the immatures and/or their predators upon arrival (A. Smith, 1976). Cannibalism has been documented in *A. mississippiensis* (Kellogg, 1929; Perkins, 1955), but evidence from large scale food studies indicates that it is extremely rare. Three analyses of the stomach contents of alligators 91 cm (3 feet) or larger from Louisiana report a total of only 5 of 935 stomachs (0.5%) containing alligator parts (Giles and Childs, 1949; Valentine *et al.*, 1972; Joanen and McNease, 1977); predators of juvenile alligators were much more

frequent in stomach contents. Modha (1967) has reported positive responses by adult *Crocodylus niloticus* (presumably of both sexes) to playbacks of juvenile calls; both cannibalism and protective behavior by adult males have been documented in this species (Cott, 1961; Pooley, 1977).

The responses of hatchling and one-year old alligators to playbacks of loop 1 are consistent with the hypothesis that high-intensity juvenile grunts (= distress calls) alert and stimulate movement by young alligators, but do not communicate alarm. Reasons for the bimodal response are not clear to me. In some cases, juveniles may have detected my presence after their initial approach and responded by moving under cover. However, this is not likely for instances in which I was well-concealed and observed identical responses. In responding to juvenile grunts, juvenile alligators may simply be alert for meaningful visual stimuli--i.e., the approach or presence of the parent female, other juveniles, potential prey or potential predators. Subsequent behavior may depend on what is encountered. If there are no visible stimuli associated with grunting (as was probably the case for most playbacks), then the probability that the vocalizing individual is separated from the pod and/or being eaten may increase. Since these are undesirable situations, cover seeking by the remaining pod members would be adaptive. If this is true then juvenile grunts would communicate distress to other juveniles only if persistent.

In addition to their initially positive responses to playbacks of distress calls, juveniles clearly are attracted to calls of juveniles which have been captured and are unequivocally in distress.

The probable explanation for this must be the likelihood that the parent female will also respond (Table 5-1). Juveniles moving toward the source of vocalizations would therefore be reducing their separation from the parent. Presumably, proximity to the adult female offsets any increased risks of predation incurred in moving toward locations where predators are potentially present. Adult alligators are known to consume virtually all known predators of hatchlings (McIlhenny, 1934, Valentine *et al.*, 1972; Joanen and McNease, 1977). Hatchlings which fail to respond to vocalizations may also risk separation from the pod; the disadvantages of this (in terms of increased probability of future predation) may be greater than the potential disadvantages of a positive response.

The results of my limited trials using different rates of grunting suggest that the extent to which juveniles are initially alerted by grunts depends on the repetition rate rather than the frequency spectrum of these grunts. Amplitudes and frequencies of the calls were identical for all trials, but it remains possible that the increased response to loop 4 was a response to the increased number of calling individuals on this recording. If so, this would imply that juveniles could successfully distinguish the grunts of different individuals on the basis of slight differences in frequency. Garrick and Garrick (1978) have found that the repetition rate of grunts of distressed *Caiman crocodilus* is relatively stable (within broad ranges) between 18 and 33°C. Ten minutes after emergence into morning sunlight, basking alligators could have body temperatures 5°C higher than juveniles remaining in the water, and differences between adults and juveniles

in some situations could be even greater (E. Smith, 1976; Smith and Adams, 1978). If repetition rate of grunting conveys information, then it is important that the rate-temperature relationship observed in *C. crocodilus* be valid for *A. mississippiensis* as well, in order to reduce signal ambiguity (Garrick and Garrick, 1978).

Arena playbacks provided additional evidence that calls given in distress contexts did not necessarily convey alarm when played back in other contexts. The hypothesis that grunts of juvenile *A. mississippiensis* function as contact calls was also supported by the results of the arena tests, although these were poorly controlled. Juvenile alligators had no difficulty in locating the source of the sounds, and in individuals which gave B responses, only momentary confusion was produced by switching speakers. When tested in the same arena in the absence of auditory cues, juvenile alligators used celestial cues to demonstrate a significant preference for directions normal to their home shorelines (e.g., Y-axis orientation--P. Murphy, 1978). The results from my tests indicated that individual alligators in novel situations respond to auditory cues more readily than to celestial ones.

CHAPTER VI SUMMARY AND CONCLUSIONS

The behaviors of juvenile *Alligator mississippiensis* are effective in actively maintaining group cohesion for at least 9 months after hatching. The most important of these behaviors is the juvenile grunt, which functions as a contact call. Grunts are given most often in situations likely to result in separation of individuals from the group, i.e., during or in response to movement, and during nocturnal foraging. They are used by isolated individuals to orient and return to the group, and are given in response to other stimuli of interest to alligators, such as prey, the approach of potential predators, and the approach or movements of the female. Increases in grunting also occur at two predictable intervals, morning and evening emergences, and follow long periods of relative silence during which pod members have become more widely separated. The social bask is particularly important in maintaining cohesion, and the reaggregation of juveniles following dispersal by an intruder is quite similar. All of these behaviors indicate that while the presence of an adult female is an important stimulus in promoting pod cohesion and coordinating movements, pod cohesion can be effectively maintained in her absence.

The use of regularly repeated signals which have continual effects on the receiver has been referred to as tonic communication by Schleidt (1973). Tonic communication via contact calls such as those used by

alligators is also characteristic of waterfowl and gallinaceous birds when maintaining contact with mates or siblings (Collias, 1960; Stokes, 1967). Schleidt (1973) has hypothesized three main functions for tonic communication. The first is the use of calls as a beacon or homing signal, which has been documented for *A. mississippiensis*. A second function may be that repetition insures receipt of a signal over background noise, especially if receivers can use signal averaging. This might be another way of accounting for the increase in VAH of pods of alligators after sundown; the loss of visual contact would make the receipt of at least some vocal signals more important, particularly during a period of rapid movement. Finally, Schleidt has suggested that repetition of signals for different periods or at different rates may convey different information than individual signals; this is suggested in *A. mississippiensis* by the bimodal responses of hatchlings to playbacks.

The use of juvenile grunts by predators may become a problem when rates of vocalization increase. One playback of juvenile alligator grunts on Payne's Prairie attracted a raccoon, *Procyon lotor*, from over 100 m away to within 20 m of the speaker. In *A. mississippiensis*, a reduction in the number of grunts/series is concurrent with the rise in VAH. This might represent a partial solution to the predation problem; single grunts would provide general location information to other pod members, but would be more difficult to locate than a longer series.

One of the major advantages ascribed to group behavior is that it results in a reduction in each individual's risk of predation. This may result from increased likelihood of predator detection (Vine, 1971), the reduced likelihood of any one group member being chosen over another

("selfish herd" hypothesis, Hamilton, 1971) and the possibility of group coordination in escape which may confuse or alarm potential predators (see Wilson, 1975, Chapter 3). I do not consider either of the latter two to be likely for *A. mississippiensis*. Pods of alligators scatter rather than contract when approached; their escape responses are coordinated only in the sense that juvenile grunts increase, and in any case the submergences and cover-seeking behaviors normally used suggest a cryptic strategy rather than an escape response intended to confuse or alarm. Increased predator detection is a likely result of grouping in *A. mississippiensis*, and since pod members are normally siblings it is also possible that kin selection has favored the use of juvenile grunts as alarm calls in distress contexts (Staton, 1978). It is much more likely, however, that grouping in *A. mississippiensis* is related to the large amount of parental care, including defense against predators, that pods receive. As discussed in Chapter 4, the restricted home range of adult female alligators makes it likely that even those females which are not always in attendance would potentially be close enough to their pods to respond to a juvenile in distress. The fact that juveniles first begin to disperse significantly from the den in June when nesting begins is circumstantial evidence that there may be some expectation of parental care until this time.

Female *A. mississippiensis* may be involved in reproductive activities including parental care virtually all year, although there is individual variation in female solicitude toward nests and young. The reproductive effort of female alligators begins with nest construction in June, and maintenance of the mound, including repair following

predation, continues through the entire incubation period for some females. Some females actively defend the nest, using a consistent ritual which includes displays also used in other intra- and interspecific agonistic encounters. Nests are opened by the female and some young are transported to the water in her mouth. Subsequent care of the young may involve regular attendance by the female up through the following year. During this period, young are led through small pools created by the female until they arrive at her den, where they overwinter. Communication between parent and offspring involves a positive response by the young to the sight of the female as well as their use of distress calls to attract her; females use vocalizations to attract young to them. Active defense of pods involves ritualized threats similar to those used during nest defense; protective females may be able to distinguish young in distress from other pod members. Juveniles in distress are not only protected prior to predation, but in some instances retrieved and returned to the pod by the female.

A variety of evidence from recent studies of other crocodilians suggests that the behaviors mediating pod cohesion and parental care in *A. mississippiensis* may be widespread throughout the Crocodylidae (Chapters III, IV and V). It is significant that while no other crocodilians have been as well studied as *A. mississippiensis*, all parental behaviors described above (including nest opening, mouth transport of young by adults, pod formation, attraction of adults to calls of juveniles, and vocalizations by juveniles in response to disturbances, approaches of adults and during feeding) occur in at least one other crocodilian species and usually in members of both the Alligatorinae

and the Crocodylinae. Some differences, probably related to habitat, clearly occur. For example, Garrick and Lang (1977) have suggested that there may be slightly greater emphasis on vocal communication in marsh-dwelling species such as *A. mississippiensis*, while visual signals may play a greater role in crocodilians which occupy larger water bodies, such as *Crocodylus niloticus*. Possible differences in formation and duration of pods in crocodilians from lotic versus lentic habitats have also been discussed (Chapter III). Nevertheless, a basic system that involves parental care of a coordinated social group of juveniles and is mediated by vocal communication is typical of the family. Sound spectrographs of juvenile grunts of all species of crocodilians studied are strikingly similar (Campbell, 1973; Herzog and Burghardt, 1977; Deitz, unpublished data). Nests opened at hatching by *Caiman crocodilus* (Staton and Dixon, 1977), *Crocodylus porosus*, (Webb, 1977), *Crocodylus moreletii* (Hunt, unpublished data) and *A. mississippiensis* appear identical, and it has been suggested that the nest-opening responses of crocodilians may be quite stereotyped (Deitz and Hines, in press).

The behavioral similarities of the Alligatorinae and the Crocodylinae are of considerable evolutionary significance, for they provide convincing evidence that their common eusuchian ancestor, at least, possessed well-developed systems of juvenile social behavior and parental care. The Alligatorinae and the Crocodylinae have been distinct since the late Cretaceous (Siil, 1968); this suggests a considerably earlier origin for parental care and juvenile social groups, which must have been fairly advanced by the time of the split. The behaviors of the extant crocodilians *Tomistoma schlegelii* (Tomistominae, Crocodylidae) and *Gavialis gangeticus* (Gavialidae) are almost entirely unknown; the

young of both species emit typical juvenile grunts (H. Campbell, pers. comm.; C. A. Ross, pers. comm.). Some additional evidence of the behavioral sophistication of the early Eusuchia is provided by the similarities in adult social signals of *A. mississippiensis*, *Crocodylus acutus* and *C. niloticus* (Garrick and Lang, 1977). The behaviors of extant Crocodilia may thus constitute better evidence for the existence of complex social behavior in Mesozoic thecodonts than inferences based on dinosaur morphology (Brattstrom, 1974; Farlow and Dodson, 1975), physiology (Bakker, 1975), or fossilized tracks (Ostrom, 1972).

Some conjectures concerning the origin of parental care in the Crocodilia can be made, although it is obviously impossible to do more than speculate on the origins of behaviors which are at least 65 million years old. The most reasonable guess would be that parental care of the young developed as an extension of care of the eggs. Egg-brooding appears to have evolved several times in Recent reptiles: it occurs in several skinks, *Eumeces* (Smith, 1946; Evans, 1959), in the king cobra, *Ophiophagus hannah* (Oliver, 1956) and in *Python molurus*, where it also involves metabolic changes in the brooding female (Vinegar *et al.*, 1970). It does not seem unreasonable to postulate its existence in the earliest crocodilians or in other thecodonts. Active protection of the eggs might readily evolve in response to high nest predation; colonial nesting by Recent *Crocodylus niloticus* (Cott, 1961) might represent another such response. Cott (1961) also points out that young *C. niloticus* cannot escape from most hole nests unaided, and I have found hatchling *A. mississippiensis* that were not removed by the parent dead in mound nests (Deitz and Hines, in press). Thus, even

if active defense did not always occur, the nesting strategy of ancestral crocodilians might have required at least a return by the parent at hatching.

Protection of young thecodonts after hatching would most likely also develop in response to predation. Trivers (1972) has reasoned that once a female has invested heavily in her offspring, further investments will be strongly selected for to protect this initial commitment. If this is true, early crocodilians would have progressed readily to post-hatching care. An analysis of parental investment by Maynard-Smith (1977) suggests that even though initial investments by males are lower, male parental care is also expected in situations where predation on juveniles is severe. Data on natural mortality of young *Caiman crocodilus* and *Crocodylus moreletii* would be of great interest in this regard, since substantial parental care has been observed in captive males of these species. Protection of scattered hatchlings would be difficult and probably ineffective against most predators. If parental protection is important to juvenile survivorship, aggregations of juveniles would also be favored, since these would be advantageous to both protective parents (which could more efficiently protect more young) and individual offspring (whose probability of being close to and protected by the parent would increase in a group). The possibility that crocodilian juvenile groups evolved in the absence of parental care is suggested by the existence of juvenile social aggregations in *Iguana iguana* (Burghardt *et al.*, 1977). However, the positive responses of juveniles to the sight and vocalizations of adults and the protective responses evoked in adults by juvenile distress calls make it more

plausible that the protective parent has been the major selective advantage to pod formation in crocodilians.

One last consideration that has received far too little discussion is the role of learning in the behavior of the Crocodilia. Learning in crocodilians has been largely neglected, despite rampant speculation on the mental capacities of dinosaurs and indications that when their physiology is taken into consideration, crocodilians learn quite rapidly (Northcutt and Heath, 1971). Throughout this study of *A. mississippiensis* there is evidence that the behaviors of individuals are readily modified to suit different environments and conditions. Behaviors such as parental defense of young may be 65 million years old, yet individual females are able to eliminate defensive behavior in response to human disturbance without altering other parental behaviors such as nest opening or creation of pools for juveniles. The ontogeny of crocodilian behavior patterns will unquestionably be difficult to study, but such studies should produce some interesting results.

Crocodilians have survived and flourished as aquatic carnivores while their terrestrial relatives have become extinct. The development of mutable reproductive and juvenile social behaviors that provide for extensive parental care in a variety of environments has probably been an important factor in the evolutionary persistence of this order. Here, perhaps, are opportunities to study ecological influences on behavior which would also provide some important insights into the evolution of reptilian and avian behavior. Let us hope that crocodilians will be persistent enough in the future to allow such opportunities.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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