Nocturnal behaviour of American Alligator *(Alligator mississippiensis)* in the wild during the mating season

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THE American Alligator is by far the most studied species of crocodilian. However, previous research on its behaviour has been conducted only in captivity (Garrick et al., 1978; Garrick & Lang, 1977; Vliet, 1989; Huchzermeyer, 2003) or in daytime hours (Watanabe, 1980). In the course of night time observations of alligators in the wild in the spring months of 2006-2009, two undescribed forms of social behavior were observed.

METHODS AND MATERIALS

Regular observations were made at four locations (Fig. 1) in the southern part of the Florida peninsula, at 0-2 m ASL. The locations were selected to represent the wide range of natural habitats occupied by alligators in the area. Each of the four locations was observed for one 16-hour period (approximately 18:00-11:00) each week from March 26 until May 17, 2006, except as noted below. These locations were: 1) Arthur R. Marshall Loxahatchee National Wildlife Refuge (ARMLNWR, 26˚30'N, 80˚15'W), a network of artificial and natural channels in seasonally flooded marshland; 2) An unnamed lake at the edge of Fakahatchee Strand State Preserve (FSSP, 26˚49'N, 81˚25'W), surrounded by tropical hardwood forest; 3) A natural stream 3-7 m wide and about 1 m deep in Big Cypress National Preserve (BCNP, 25˚47'N, 81˚06'W), surrounded by seasonally flooded forest of Bald Cypress (*Taxodium distichum*); 4) An unnamed lake with a network of radiating channels on private land near the northern edge of BCNP (26˚15'N, 81˚15'W), surrounded by wet marshland.

Water levels at sites 3 and 4 fell dramatically during the observation period. At site 3, the channel dried out completely and all alligators moved elsewhere, so the observations were discontinued on May 5. In May, some observations were conducted for 36 hour periods (two nights and the intervening daylight period). Occasional observations were also made at other locations in BCNP, as well as at Taylor Slough and Shark Valley in Everglades National Park (25˚23'N, 80˚36'W and 25˚39'N, 80˚46'W, respectively), and at forest ponds ("gator holes") in Picayune Strand State Forest (PSSF, 26˚07'N, 81˚31'W).

In 2007-2008, additional observations were made at various locations (Fig. 1) in Ocala National Forest, Florida (ONF, 29˚20'N, 81˚40'W) and Savannah National Wildlife Refuge, South Carolina (SNWR, 32˚11'N, 81˚20'W). In 2009, occasional observations were made in Aransas National Wildlife Refuge, Texas (ANWR, 28˚15'N, 96˚55'W), St. Catherine Creek National Wildlife Refuge, Mississippi (SCCNWR, 31˚22'N, 91˚42'W), Cat Island National Wildlife Refuge, Louisiana (CINWR, 30˚89'N, 91˚20'W), and Anacoco Floodplain, Louisiana (AFP, 31˚24'N, 93˚24'W). Unless specified, all information below refers to 2006 Florida observations.

Total observation time in 2006-2009 was over 1200 hours, including 380 hours of night time observations. Alligators were observed either from the shore or from an inflatable kayak. A small headlamp with a red filter was used on moonless nights. The animals seemed remarkably indifferent to the presence of an observer, often courting, bellowing or mating within 1-2 m of the kayak.

Animals were counted at 20 min intervals and all observed behaviours were recorded. During large gatherings, when recording all behaviours for all animals was impossible, estimates of the frequency of observed behaviours were made by counting the occurrence of a behaviour during an

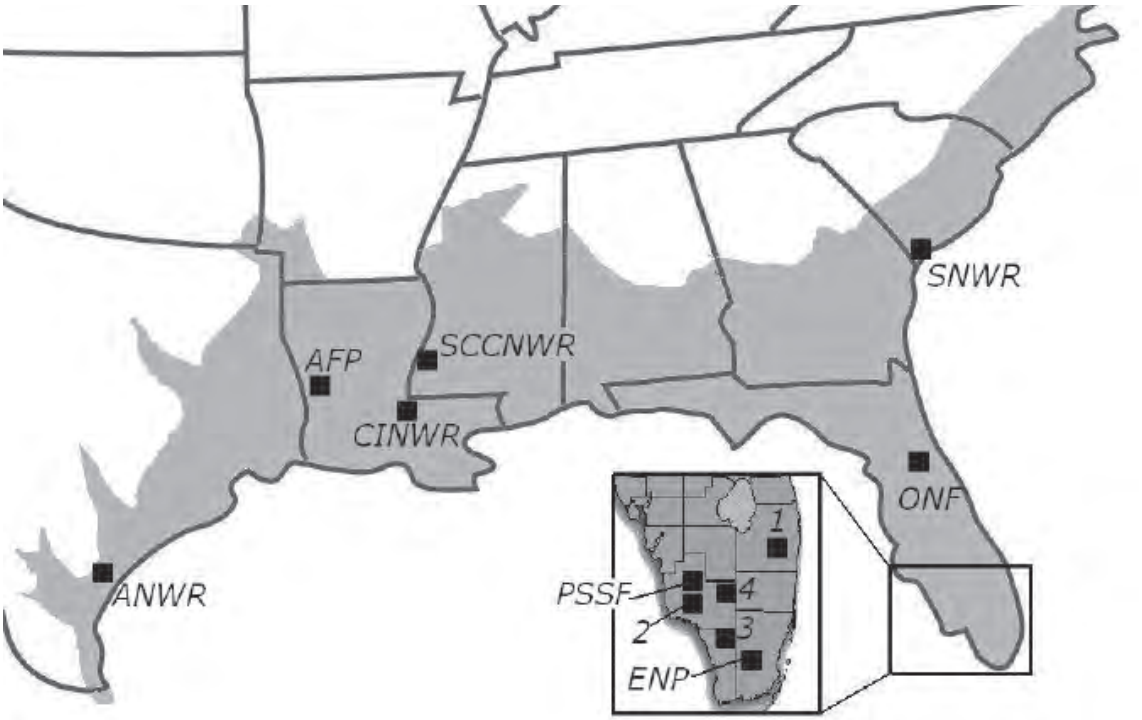

Figure 1. Study sites in the southeastern United States. Sites of regular observations: 1 – Arthur R. Marshall Loxahatchee National Wildlife Refuge, 2 – Foxahatchee Strand State Preserve, 3-4 – Big Cypress National Preserve. Sites of irregular observations: ANWR – Aransas National Wildlife Refuge, AFP – Anacoco Floodplain, ENP – Everglades National Park (Taylor Slough and Shark Valley), CINWR – Cat Island National Wildlife Refuge, PSSF – Picayune Strand State Forest, SCCNWR – St. Catherine's Creek National Wildlife Refuge, SNWR – Savannah National Wildlife Refuge. Approximate range of American Alligator shaded.

arbitrarily selected 5 min interval. Size of animals was visually estimated as belonging to half metre interval size classes of total length: less than 0.5 m, 0.5 to 1 m, and so on. Unless specified otherwise, sizes below are given by the lower limit of the size class. Keeping track of individual animals was usually difficult, so only twelve alligators with easily recognizable features were recorded for more than one night with certainty. The lengths of channel stretches recorded below were all measured by pacing. Areas occupied by gatherings were visually estimated. Video, photographic and audio recordings of various types of behaviour were obtained.

RESULTS

Courtship Gatherings

At all sites, mating-related activities such as bellowing choruses, swimming in pairs, chasing, and snout touching (Garrick et al., 1978) were first observed during the week of April 9-15. As water levels dropped, alligator numbers at sites 2-4 increased rapidly, from 5-10 in late March to 50-100 in late April, and the animals concentrated in areas with deep water. At site 1, where water levels did not change, the animals also concentrated in one stretch of the main channel, 200±20 m long.

From mid April until mid May, alligators at all four regular study sites and at Taylor Slough gathered in large numbers, apparently for courtship (Fig. 2). The maximum number observed was 80 (at Taylor Slough), mean maximum number per gathering was 28 (Fig. 3). Each gathering occupied a well-defined area, visually estimated to be 100-600 m^2. The precise location of the gathering changed each night. At sites 2-4 and at Taylor Slough, the animals had limited choice of locations, but at site 1 all their gatherings took place within only

Figure 2. Courtship gathering of American Alligators in Big Cypress National Preserve, Florida. Note two males resting their chins on the backs of females as part of courtship.

one section of the main channel, 100±10 m long, which did not differ in visible features from other sections. At its maximum, the abundance of animals (determined by dividing the total area occupied by the gathering by the number of animals present) exceeded one animal per 10 m^2. For comparison, the density of alligators in the remaining parts of the lake/channel (determined by dividing the total water area by the number of animals counted during the same night of observation) did not exceed one animal per 100 m^2, except at site 3 in the last day before it completely dried out.

On some nights gatherings were not observed. One such night was on April 24 the only rainy night during the study period. No significant association of presence/absence of gathering with water temperature (χ^2 0.75; P = >0.05) or lunar phase (χ^2 0.05; P = >0.25) was detected (Chi-squared test).

Each gathering lasted for 4-8 hours (mean duration 6 h 40 min, n = 15), but never for the entire night (Fig. 4). Most gatherings took place between sunset and sunrise, but three had formed before sunset (approximately 10, 10 and 30 min before sunset), and one continued for 15 minutes after sunrise (Fig. 5). At any given time, some animals present in the area were not participating in the gathering and remained in other parts of the lake/channel, where their activity patterns were similar to those observed on the nights with no gatherings. Alligators smaller than 1.5 m joined those gatherings only occasionally, and those smaller than 1 m were never observed to join them. Some alligators were not permanently present in the lakes where gatherings were taking place, but

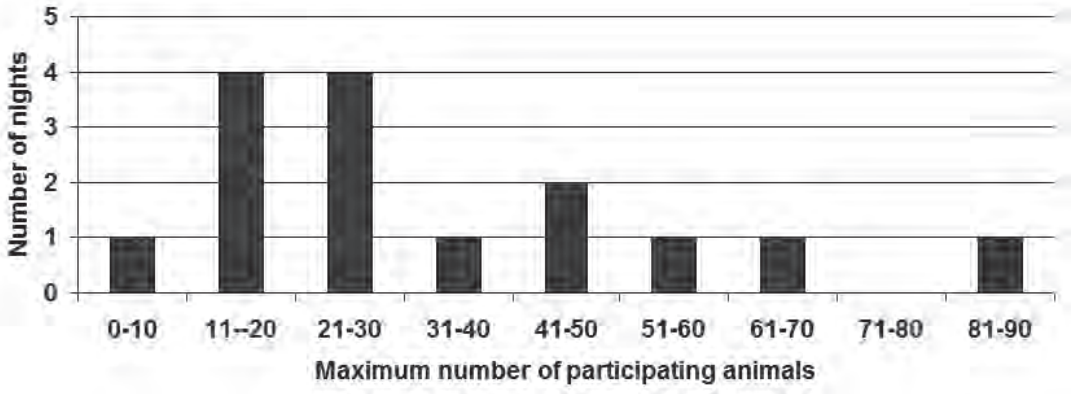

Figure 3. Maximum numbers of alligators participating in courtship gatherings.

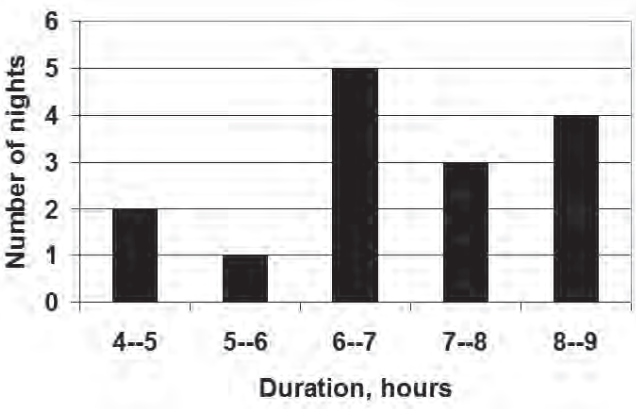

Figure 4. Duration of observed courtship gatherings.

were observed as they moved into the lake from surrounding channels shortly before or after the formation of the gathering, and left it later. Many participants arrived in pairs. Two particularly large and recognizable individuals were observed to participate in gatherings throughout the mating season, even though they were already accompanied by mates by mid April. Three other individually recognizable alligators were not observed to form pairs at all.

The gatherings were characterized by very high levels of activity. Animals spent hours swimming (mostly in pairs and trios), touching each other's snouts, chasing each other, and placing their chins on other alligators' backs. All these behaviours have been described by Garrick et al. (1978) as part of courtship. Fighting was also observed frequently (at least every ten minutes). Most fights consisted of just one or two jaw slaps and/or light bites, but some lasted for several minutes and resulted in visible injuries. One 1.5 m long alligator had a half of its upper jaw bitten off by a 2.5 m long individual and died two weeks later. Another common behaviour was swimming in circles: two animals would follow each other for a few seconds at a time making 1-3 circles with diameter roughly equal to the larger animal's length, clockwise or counterclockwise. Sounds such as deep grunts, low growls, hisses, coughs, head slaps and tail slaps (as described by Garrick et al., 1978) were

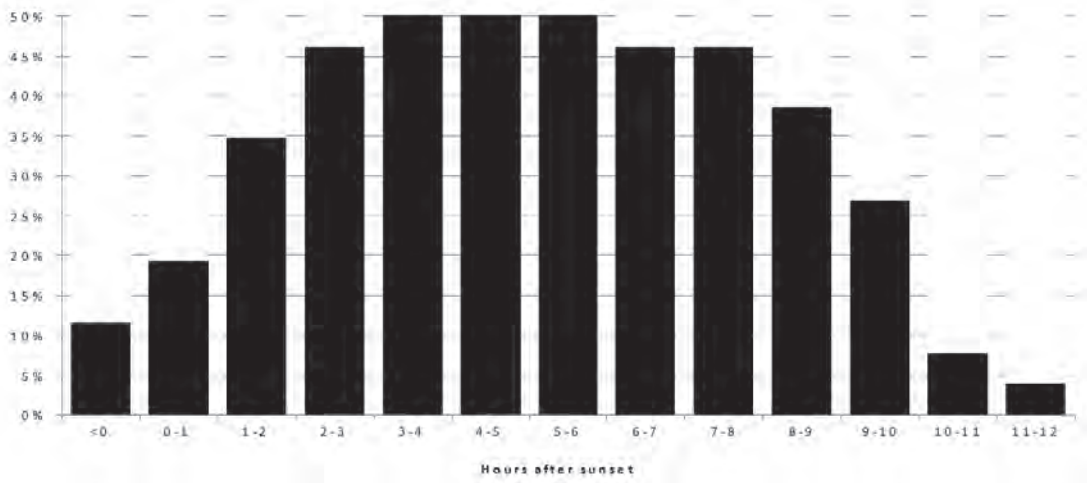

Figure 5. Percentage of nights when courtship gatherings were observed at known gathering sites at different times after sunset.

Figure 6. Cooperative feeding of American Alligators in Everglades National Park, Florida. One large animal is swallowing a fish.

used frequently (Table 1). In gatherings with more than 20 participants, each sound was heard at least once over all 5 min intervals when frequency of those behaviours was recorded. Large gatherings produced so much noise that they could be easily heard from up to 300 m away. Bellowing was never recorded during gatherings, even if they continued into daylight. Copulation was observed twice during those gatherings. On both occasions the pairs left the gathering and mated nearby away from the group (approximately 15 and 35 m). More often, copulation occurred after the gatherings (three observations before dawn and six observations during morning hours). Bellowing choruses were more than twice as likely to be observed on a morning after a gathering as on a morning that followed a night when no gathering took place (12 bellows recorded after 15 nights with gatherings, 4 after 11 nights without gatherings).

On eight occasions, alligators were observed catching or attempting to catch fish during gatherings, but their level of fishing activity was very low (in 96 hours of gatherings observed, only six fishing attempts were recorded, less than 0.1 attempt per animal per hour). Animals not involved in any type of gathering made 1-5 such attempts per hour in the water. Once a 2 m long alligator was seen trying to catch a Black Crowned Night Heron (*Nycticorax nycticorax*).

The spring of 2006 was unusual in that many female alligators had very small offspring. Normally the majority of hatchlings in southern Florida appear during the late summer. But in fall and winter months of 2005-2006 many females nested very late in season, probably after having their nests destroyed by hurricanes in 2005. In one remarkable case, a 2 m long female with a recognizable teeth pattern was seen leaving her brood of 30 cm long juveniles and swimming for two miles downstream to a place where a gathering was taking place. This behaviour was observed on one night in April and two nights in May. Each time she would leave her brood at approximately sunset, spend part of the night in the gathering, and

Type of gathering	Fishing attempts per animal per hour	Predominant sounds	Swimming pattern	Water depth at location	Minimum size of animals
Courtship gatherings	Less than 0.1	Deep grunts, low growls, hisses, coughs, head slaps and tail slaps	At least 1/3 of animals swim in pairs and trios	Deeper than 50 cm, if available	1 m
Cooperative feeding	More than 6	Jaw slaps, splashing sounds	No animals in pairs or trios	Less than 50 cm	60 cm

Table 1. Differences between cooperative feeding and courtship gatherings.

return in late morning. Possibly due to predation by Great Blue Herons (*Ardea herodias*), the number of her offspring fell from six to two during that time. She was seen in the gathering three times, but was never observed to find a mate.

In the spring of 2007, courtship gatherings were recorded in other parts of the species range: twice in ONF (at 03:20 on April 28 and at 11:55 on May 5) and twice in SNWR (at 22:20 on May 10 and at 00:12 on May 15). In all cases, the beginning and the end of the gatherings were not observed. The number of individuals present was 16, 11, 5 and six respectively. The relatively small numbers of participating animals at the two SNWR gatherings probably reflects the overall lower density of alligator in South Carolina in the northern part of its geographical range (Neill, 1971).

In the spring of 2008, more gatherings were noticed during occasional observations in ONF (four gatherings, all in pre-dawn hours) and in ENP (two gatherings, one near midnight and one at pre dawn time). One of the gatherings took place at just 10˚C air temperature (ONF, April 18), and one was at the latest date ever recorded (ENP, May 25).

In the spring of 2009, courtship gatherings were incidentally observed in the western part of the species' range: five times in ANWR (all with more than 10 animals present), twice at SCCNWR (with six and five animals), once in CINWR (with six animals), and once at AFP (with four animals). The amount of time spent observing alligators at night was approximately the same in all four locations. It appears that such gatherings are not only larger, but also more common in the southern part of the geographical range of the American Alligator.

Cooperative Feeding

Cooperative feeding was observed only in late April and May, and always in places with water depths of less than 50 cm. It was seen once at FSSP, twice at BCNP (once at each site) and five times at Taylor Slough. On each occasion, 10-50 (arithmetic mean 22.5, n = 8) alligators would gather in an area not larger than 250 m^2 or in a small pond about to dry up (Fig. 6). They would then spend 2-6 hours (arithmetic mean 3 h 20 min, n = 8) swimming in circles (usually over 5 m in diameter) in that small area and catching fish, with 2-20 jaw slaps being heard every minute. The level of fishing activity was roughly estimated as 0.1-3 fish catching attempts per animal per minute, compared to 1-5 attempts per hour in animals not involved in a gathering of any type, and less than 0.1 attempt per hour in animals in courtship gatherings. When fishing occurred on the water surface the method observed was almost always a quick lateral jerk of the head, accompanied by slapping of the jaws. Less than one in ten times, alligators made a frontal attack instead, lunging forward and catching fish with the tips of their jaws. Judging by the plumes of silt rising to the surface, a lot of fish were taken from the bottom mud. On a few occasions the fish could be identified to family as it was caught and eaten. Two fishes were Cichlids (Cichlidae); all others were Catfish (Ictaluridae). Despite the presence of many Florida Gars (*Lepisosteus platyrhincus*) at some sites, alligators were never observed to catch them. All cooperative feeding was observed between 17:00 and 09:00. Most animals were more than 1 m in length, but a few juveniles as small as 0.6 m were also seen.

Cooperative feeding gatherings could be immediately distinguished from courtship gatherings (Table 1). Swimming in pairs never took place, even though some animals arrived to the gathering in pairs. Sound signals were never recorded, except for very few low growls and hisses when one alligator accidentally bumped into another. Fights over fish happened occasionally. It was possible to tell the two kinds of gatherings apart even without seeing them: cooperative feeding produced mostly splashing and slapping sounds, while courtship gatherings were also accompanied by grunts, growls, hisses, and coughs. No gatherings intermediate between feeding and courtship types were ever observed. On one occasion at Taylor Slough, a courtship gathering and cooperative feeding were taking place at the same time within 30 m from one another and a few animals (five in two hours) were seen moving between them.

DISCUSSION

Both cooperative feeding and courtship gatherings occasionally take place during daylight hours and can be watched by hundreds of visitors to Everglades National Park. However, these types of behaviour

apparently have never been described in scientific literature, probably because daytime observers did not recognize them as a distinct and regular type of behaviour. Cooperative feeding of other Crocodilians (see below) has been mentioned in popular literature and shown in TV documentaries but scientific descriptions are also lacking.

It seems reasonable to assume that courtship gatherings are an important part of courtship behaviour in alligators although they are not essential for pair formation (as demonstrated by successful breeding of animals in isolated ponds and in captivity). The purpose of cooperative feeding seems obvious, but the exact mechanism of the increased efficiency of group fishing is not. Sometimes the fishing area is adjacent to deeper water. So why do fish not leave when cooperative feeding begins? One possibility is that the fish (Catfish in particular) are either taken from the layer of mud on the bottom, or flushed out of mud and immediately eaten. In this case, the presence of many alligators possibly causes the remaining Catfish to hide in mud instead of leaving the area immediately. This thus would prompt alligators to flush them out one by one.

Cooperative feeding might be common among most Crocodilians that occur at sufficient population densities. Anecdotal evidence and numerous video recordings suggest that it is used by all species of genus *Caiman*, and also by the Nile Crocodile (*Crocodylus niloticus*), which employ a variety of group tactics for hunting fish and mammals. A documentary called 'Lake of a Thousand Caiman' by National Geographic shows cooperative feeding by hundreds of Black Caiman (*Melanosuchus niger*) in the Amazon. The author has observed cooperative feeding by 12 Mugger Crocodiles (*C. palustris*) that were catching Catfish in Kateraniaghat Wildlife Sanctuary, India, and by three Saltwater Crocodiles (*C. porosus*) catching a domestic pig near the city of Sorong in the Indonesian part of New Guinea.

Courtship gatherings seem to be much less common among Crocodilians. Despite an extensive literature search, interviewing crocodile researchers and professional hunters, and hundreds of hours of night time observations in the wild during the mating seasons of Nile, Mugger, Saltwater, American (*C. acutus*), Morelet's (*C. moreleti*) and Orinoco (*C. intermedius*) Crocodiles, as well as Black Caiman, no courtship involving more than four animals has been recorded or heard of. One possible explanation is that male crocodiles (Neill, 1971) and Black Caiman (P. Taylor, pers. comm.) are much more territorial than male alligators. Group courtship was observed in captivity among Chinese Alligators (*A. sinensis*) (Wang Xi, pers. comm.) and Indian Gharials (*Gavialus gangeticus*) (pers. obs.), but it is unknown if this behaviour occurs in the wild, where population density is much lower. It was never seen by the author in six nights of observing Indian Gharials in Kateraniaghat Wildlife Sanctuary during the mating season.

Group courtship can be easily observed among Yacare Caiman (*Caiman yacare*) in the Brazilian Panthanal and adjacent parts of Bolivia. During a study of caiman vocalizations in September-November of 2007, caimans were seen engaging in a frenzy of courtship in certain lakes, where 10-50 animals were present throughout the mating season, with densities of 0.5-2 animals per 100 m^2. Unlike alligators, they did not gather in particular locations at the beginning of each courtship event and dispersed at the end of it. Most individuals remained in a particular lake for weeks and participated in courtship every day from approximately one hour before sunset until sometime between midnight and dawn. Caimans did not congregate in one part of the lake, but used most of its area for courtship activities. However, if the surrounding floodplain was covered with water after heavy rains, the animals did not disperse more than 100 m away from the original lake contour until the end of the mating season. Unlike alligators, individual Yacare Caiman are easy to identify and follow due to unique patterns of facial markings. Courtship behaviour itself was very similar to that of American Alligators, as described by Garrick et al. (1978).

On January 3, 2010, an apparent courtship gathering of six Broad-headed Caimans (*C. latirostris*) was observed for most of the night at Itaipu Reservoir on Paraguay-Brazilian border. Again, the courtship behaviour was very similar to that of American Alligators and Yacare Caimans.

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