STATUS, ECOLOGY, AND CONSERVATION OF THE ORINOCO CROCODILE (*CROCODYLUS INTERMEDIUS*) IN VENEZUELA

A Preliminary Report on Investigations into the Status and Ecology of Wild Orinoco Crocodile Populations

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1. INTRODUCTION

1.1 PROJECT BACKGROUND

The Orinoco crocodile (Crocodylus intermedius) is a large riverine crocodile with a distribution restricted to the middle and lower Orinoco river drainage in Colombia and Venezuela. Accounts written by early explorers and naturalists reveal that the Orinoco crocodile was at one time very abundant throughout this region, particularly in the low-lying llanos savanna habitat, where crocodiles were one of the most characteristic faunal elements (Appun 1871, Gumilla 1741, Humboldt 1860, Paez 1868). Crocodiles were greatly feared for their size, carnivorous habits and, at times aggressive nature, and consequently were killed whenever possible. Nevertheless, crocodiles remained abundant in the Orinoco basin through the first two decades of the twentieth century.

Beginning in the late 1920's, widespread hunting of Orinoco crocodiles started in the llanos. Fueled by the European demand for crocodile hides, a large scale, organized commercial harvest quickly decimated crocodile populations throughout Colombia and Venezuela. The total number of crocodiles killed will never be known accurately, but prior to 1950, an estimated 2-4 million crocodile skins were exported from the two countries (see section 2, below). Commercial trade in Orinoco crocodile hides began to decline in the 1940's as crocodiles became increasingly scarce, and hunters were forced to search in more remote areas. The organized hide industry eventually disappeared in the 1950's due to the scarcity of crocodiles, but opportunistic poaching of crocodiles continues to this day.

Despite the cessation of commercial hunting some 30 odd years ago, little or no significant crocodile population recovery has occurred. Rather, populations continue to decline in most regions due to direct human-related mortality or indirectly via habitat destruction. Crocodiles are still viewed with great trepidation by most campesinos and are killed when they are seen as a threat to local residents or their livestock. Additionally, crocodiles drown in illegally set seine or gill nets, or are shot simply for "sport," or for selling the hide. In many parts of the llanos, the expansion of agro-industrial areas is leading to significant habitat deterioration. Complete habitat loss, via draining or river channelization is also a severe problem for at least one major crocodile population (Rio Cojedes/Sarare)(see section 5).

Although Orinoco crocodile populations were for some time known to be severely depleted, few data were available to assess population status or trends. The first large-scale attempts to evaluate population levels began in the 1970's. Surveys in both Colombia (Medem 1981) and Venezuela (Godshalk 1978, 1982) found crocodiles to be extremely rare or completely absent from large parts of their former range (see section 3.4). In 1984, the Orinoco crocodile was placed on the list of the world's 12 most endangered species of animals by the International Union for Conservation of Nature and Natural Resources (IUCN).

Although there was much general interest in the development of a conservation program for the Orinoco crocodile, little was accomplished until 1984 when the Venezuelan Fundacion para la Defensa de la Naturaleza (FUDENA) and Tomas Blohm combined efforts to establish a crocodile research center on Hato Masaguaral, Guarico state, in the Venezuelan llanos. The original function of the center was to captively breed and rear crocodiles for future reintroduction into the wild. However, with funding from international conservation organizations such as Wildlife Conservation International (New York Zoological Society), World Wildlife Fund (US) and WWF (International), investigations of the status and ecology of wild crocodile populations began in 1985.

This report outlines the results of work accomplished through the Hato Masaguaral center during the period October 1984-June 1987 (J. Thorbjarnarson, G. Hernandez, principal investigators). The objectives of the report are the following: 1) summarize the historical background of crocodile hunting in Venezuela and Colombia, 2) review the present status of Orinoco crocodiles, with particular attention to the most recent survey work done in Venezuela, 3) provide a general overview of Orinoco crocodile ecology, and 4) suggest conservation measures that will better ensure the long-term survival of Orinoco crocodile populations.

1.2. TAXONOMIC RELATIONS AND SPECIES IDENTIFICATION

The Orinoco crocodile (Crocodylus intermedius, Graves) is one of 4 New World members of the family Crocodylidae. The other 3 species are: Morelet's crocodile, C. moreletii (Atlantic coast of Mexico, Belize, Guatemala), the Cuban crocodile, C. rhombifer (Cuba and the Isle of Pines), and the American crocodile, C. acutus (circum-Caribbean region, Pacific coast from Mexico to Peru). Although it is potentially sympatric with only one other species of crocodile (C. acutus in the region of the Orinoco delta), the Orinoco crocodile has frequently been confused with other crocodilians, especially C. acutus (Brazaitis 1971, Thorbjarnarson and Franz 1987). A number of specimens of C. acutus in zoological or museum collections in the United States have been misidentified as C. intermedius. The skull drawing labelled C. intermedius in the classic work of Mook (1921) was actually from an African C. cataphractus, and this error has been repeated several times, most recently in the CITES identification manual for crocodilians (Wermuth and Fuchs 1984). Much of the prior difficulty identifying specimens of C. intermedius stems from poorly documented information concerning its distinctive morphological characteristics. Previously, much emphasis was placed on snout morphology (narrow snoutedness) in distinguishing it from C. acutus. While snout morpholgy can be distinctive, the most useful characteristics in separating the two species are:

1. Dorsal scalation: C. intermedius has 5-6 dorsal (rarely 4) scutes arranged contiguously in any one mid-dorsal transversal row. In C. acutus the arrangement is much more irregular, with a normal maximum of 4 (rarely 5 or 6) in any one mid-dorsal transversal row.

2. Cranial morphology: in *C. intermedius* the mandibular symphasis extends to the level of the 5th or 6th mandibular tooth (4th in acutus), and has a typically concave snout profile anterior to the orbits. In *C. acutus*, (subadults and adults have a distinctive preorbital hump, giving the snout a more convex profile.

2. HISTORY OF THE HIDE TRADE FOR ORINOCO CROCODILES

Historically, crocodiles were killed by indigenous peoples and early European settlers because they represented a danger to people and their livestock (Gumilla 1741, Humboldt 1860, Paez 1868). Crocodiles or their by-products were frequently used for various purposes. During the early dry season Indians would, and in some areas still do, excavate crocodile nests and eat the eggs. Eggs (and the crocodile penis) were widely sought as a cure for asthma. Crocodile fat was used to produce an oil used in lamps, to treat bruises or cutaneous diseases of horses, or as a cure for colds. Crocodile teeth were often taken and worn in a necklace to protect the wearer from danger (especially snakes), or worn as a collar by teething babies to bring health throughout life. The meat was apparently never eaten much by settlers or Indians, who would regularly eat *Caiman* and *Paleosuchus*. Crocodiles were also killed for "sport" by Europeans, and at times ranch owners would offer a bounty (Paez 1868).

According to T. Blohm (pers. comm.), the first commercial utilization of Orinoco crocodile skins began in the early 1800's, when they were sought to make industrial machine belts for certain heavy machinery in England. The first actual hide hunting for producing leather goods was started in 1894 by a North American company in El Yagual (Apure State)(Medem 1983, citing Verstraelen 1939). Crocodiles in the Apure and Arauca rivers were killed during daylight hours using firearms. However, this venture was apparently less than a commercial success and soon shut down. Intensive commercial hunting did not begin until the late 1920's and rapidly spread during the early 1930's, when the introduction of nocturnal hunting techniques made it a much more viable enterprise.

Beginning in the early 1930's, commercial exploitation of crocodile hides became a lucrative, widespread industry in the llanos of Colombia and Venezuela. The principal rivers in Venezuela from whence crocodile skins were obtained were the: Orinoco, Apure, Arauca, Guarico, Portuguesa, Cunaviche, Capanaparo, Cinaruco and the Meta. The major centers for crocodile skin commerce in Venezuela were San Fernando, Caicara, and La Urbana. In these towns, buyers would purchase skins, then ship them downstream to Ciudad Bolivar (formerly Angostura) for export. The major importing countries were Germany, France, and the United States, with lesser numbers going to England, Italy, Holland and Japan. In addition to the crocodiles killed in Venezuela, crocodiles killed in the Colombian sections of the Arauca, Capanaparo and Cinaruco rivers were brought downstream and sold in Venezuela. Crocodile skins from the Rio Meta, Casanare,

Vichada and Guayabero-Guaviare systems were sold in Villvicencio, Colombia (Medem 1983).

Crocodile hunting was done primarily in the dry season, when crocodiles would concentrate in the main river courses, generally on nights with little or no moon. Working from dugouts (curiaras), the caimaneros would slowly approach crocodiles floating in the water, and harpoon them usually in the neck just behind the skull. The caimaneros became so practiced at this that they could completely severe the spinal cord, instantly killing the crocodile. At first, medium sized (2-2.5 m total length-TL) crocodiles were the most sought after because they produced higher quality hides with fewer osteoderms (Medem 1983). Nevertheless, larger crocodiles were taken whenever possible. According to Sr. Nouble Seguias of Caicara del Orinoco, 15 foot (4.6 m TL) crocodiles were commonly sold in that town. Rarer were the 18 ft (5.5 m) skins, and extremely rarely one would see skins from 21 ft (6.4 m) crocodiles. During the first years of extensive hunting (1930-3), caimaneros operated chiefly in the the more accessible, major river systems (e.g. Orinoco, Apure). When crocodiles became scarce in these areas, the caimaneros had to hunt in more remote regions. For instance, near Caicara del Orinoco, the caimaneros hunted the main Orinoco channel during the first 3 years of operation (1930-3). During the first year alone over 3000 crocodiles were taken from the river near Caicara. A team of caimaneros in curiaras could, in one night, kill up to 70-80 crocodiles, but 35-45 was more common. The crocodiles would be quickly skinned, and the carcasses left to rot along the river banks. However, Medem (1983) reports that in some instances, certain crocodile by-products were utilized (fat for making soap, teeth for ornaments, cloacal/submandibular musk glands for perfume). After 1933, few crocodiles remained in the main Orinoco river near Caicara, and hunting shifted to areas where crocodiles could still be found in exploitable concentrations, such as more remote rivers, smaller tributaries, or adjacent oxbow lakes (Pedro Ramon Castro, pers. comm.).

The peak of skin commerce was reached soon after crocodile hunting began. The peak years for exports were 1930-34, and declined slowly thereafter through the late 1940's. Commercial trade continued, but at a much lower level through the 1950's, and some professional caimaneros still continued operating into the 1960's (Medem 1983). Caimaneros were reported to have worked the Rio Cinaruco during the early 1960's (Godshalk 1978), and unconfirmed reports suggest hunting in the Rio Caura peaked during the mid to late 1960"s.

The total number of crocodiles killed during the period of commercial exploitation is impossible to estimate accurately. Reported export figures grossly underrepresent the actual volume of trade. Besides inadequately representing skins sold, they do not account for crocodiles that were killed and subsequently lost, or escaped the hunters while being mortally injured. Medem (1981) reports published Colombia export figures of 235,200-254,200 skins, but stresses that the reports are incomplete and represent an absolute minimum. Data for Venezuela are similarly incomplete, and furthermore are listed in weight of skins exported as opposed to number of hides, giving a total of 2,173,707 kg exported between 1929 and 1963 (Mondolfi 1965).

According to Medem (1983), based on information from Don Jose Faoro, one of the two principal skin buyers in San Fernando, during the peak years of 1930-31, 3,000-4,000 skins a day would be sold in San Fernando alone and the total number of skins to pass through San Fernando during this period was approximately 750,000. Considering that San Fernando was only one of three main centers of skin commerce in Venezuela, an absolute minimum of 1 million skins were exported from Venezuela alone. A very conservative estimate of the total number of skins exported from the two countries would be some 2 million, but the true figure could easily be twice that many.

Today, some crocodile poaching still continues, although not in the widespread, organized fashion of the past. Crocodiles are killed opportunistically, and the skins sold usually through Colombia. However, buyers have also been reported in Venezuela, especially San Fernando. The region where most illegal hunting occurs is the Rio Meta, along the Colombian border, with skins being sold in Puerto Carreno (Godshalk 1982).

3. STATUS AND DISTRIBUTION

3.1. LEGAL STATUS

The Orinoco crocodile is legally protected in both Colombia and Venezuela. In Colombia, legal protection is in the form of 2 resolutions, one by the Ministerio de Agricultura (Resolucion 411, 16 July 1968), and another by the Natural Resources department, INDERENA (Resolucion 573, 24 July 1969)(IUCN 1982). Both resolutions prohibit the killing of crocodiles.

In Venezuela, crocodiles were first legally classified under the 1944 Ley de Pesca, which required a permit for hunting. The 1970 Ley de Fauna prohibits the killing of crocodiles (Godshalk 1982).

Although crocodiles are legally protected throughout their range in both Colombia and Venezuela, this legislation has had little or no effect on the continued poaching of crocodiles. Enforcement is difficult because much of the hunting occurs in remote areas. But the killing, capture and sale of crocodiles even continues in areas where the enforcement of exisiting laws is easily accomplished.

On an international level the Orinoco crocodile is on Appendix I of the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). This listing strictly prohibits commercial trade of Orinoco crocodiles among member nations.

3.2. FORMER CROCODILE DISTRIBUTION

3.21. Colombia

The distribution of the Orinoco crocodile in Colombia has been reviewed by Medem (1981). He reports that the former range of the Orinoco crocodile in Colombia was an area of 252,530 square kilometers between the Rio Arauca in the north, and the Guayabero-Guaviare system to the south. The westernmost distribution of crocodiles was said to be the Rio Duda, a tributary of the upper Guayabero. Crocodiles were distributed throughout the principal river systems in the western llanos of Colombia: the Rio Arauca, Meta, Vichada, and the Guayabero-Guaviare. Crocodile density was reported to be high in the Arauca/Meta/Guayabero systems, but lower in the Vichada and its tributaries (Medem 1974). Crocodiles were also found in the headwaters of several rivers that lie principally in Venezuela (e.g. Capanaparo, Cinaruco).

Within this range, crocodiles were probably at one time found in virtually all of the Orinoco tributaries that cross the Colombian llanos. Medem (1974, 1981) reports a minimum list of Colombia rivers where crocodiles were known to be found (Table 1).

3.22. Venezuela

As in Colombia, the former distribution of the Orinoco crocodile in Venezuela included the Orinoco river and virtually all its major tributaries in the llanos. Apparently, crocodiles also extended far up many llanos rivers and into surrounding piedmont areas in the foothills of the Andes (e.g. Rio Tucupido, Portuguesa state), Crocodiles also could be found in most of the southern Orinoco tributaries that pass through savanna and heavily forested regions (e.g. Rio Cuchivero, Rio Caura).

The biggest questions today concerning the past distribution of crocodiles are the up- and downstream limits within the Rio Orinoco drainage.. Humboldt (1860) commented on the apparent lack of crocodiles from the upstream section of the Orinoco and states that crocodiles are only found up to the vicinity of the "Rio Jao" (between San Fernando de Atabato, and the mission at Esmeralda). Humboldt also states that crocodiles were found in the Rio Ventuari, but not in the Brazo Casiquiare. Recently, there have been some unconfirmed reports of crocodiles in the Casiquiare, but it is clear that if crocodiles ever did exist in the area it was at very low population levels.

Although one of the common names of C. intermedius is the Orinoco Delta (or Venezuelan Delta) crocodile, very little information exists on its presence in the delta region. Large crocodilians are known to have been seen in the delta, but their specific identity could be either C. acutus, C. intermedius, or even Melanosuchus niger (S. Gorzula, pers. comm.). Four C. intermedius (2 male/2 female) were collected for a zoological park in Puerto Ordaz from the upstream delta region in 1959 (Ramierez et al. 1977). Also unconfirmed reports indicate that crocodiles held in private homes in Tucupita are all C. intermedius (E. Cartalla, pers. comm.).

3.3. STATUS AND DISTRIBUTION: 1970-1984

3.31. Colombia

The most recent data on the status of Orinoco crocodiles in Colombia is that of Medem (1974, 1976, 1981). During 1974 and 1975, Prof. Medem undertook a census of crocodiles in the western llanos of Colombia, financed through WWF. The census was based principally on ground surveys, but also included 800 km of aerial surveys in the Intendencia de Casanare (Medem 1981).

Based on this survey, Medem reported the status of crocodiles to be critically low. The number of remaining adult crocodiles was estimated to be only 280 in all of Colombia (Intendencia de Arauca-180, Comisaria de Casanare-49, Departamento Meta-14, Comisaria de Vichada-37). Medem noted that this was not an absolute count, but suggested that no more than 500 individuals (adults and juveniles) were not detected during the survey (Medem 1981). This would suggest a maximum total of fewer than 800 adult crocodiles remaining in the country.

3.32. Venezuela

Beginning in the late 1940's, concern arose regarding the effects of the intensive hide hunting and the resulting extreme scarcity of Orinoco crocodiles (Blohm 1948, Mondolfi 1957, Medina 1960). The extremely depleted state of crocodile populations was further emphasized in later publications (Mondolfi 1965, Donoso Barros 1966a, 1966b, Rivero Blanco 1968, King 1973, Blohm 1982). Although it was widely recognized that Orinoco crocodiles were an endangered species, most status accounts were anecdotal and no quantitative survey data were available.

The first large-scale attempt to clarify the status of the Orinoco crocodile in Venezuela was that of Godshalk (1978, 1982), through the sponsorship of FUDENA. Survey results were based primarily on interviews with people knowledgeable about fauna, talks with campesinos, and motorized dugout surveys of several rivers in the llanos region (Tinaco, Cojedes, Portuguesa, Orinoco, Capanaparo, Cinaruco, and Meta rivers).

The results of this survey definitively showed that Orinoco crocodiles are extremely rare in Venezuela. A total of only 273 adult crocodiles were located in the survey area (based primarily on a tally of crocodiles known to riverside dwelling campesinos). Even more alarming, Godshalk reported little evidence of reproduction or recruitment of immature crocodiles into the already greatly reduced populations. One notably positive result of the survey was the discovery of a relatively large, previously unknown crocodile population in the Rio Cojedes. Based on these survey results, Godshalk estimated that the adult crocodile population in Venezuela was approximately 1,000 (IUCN 1983). A list of rivers and caños (small rivers) reported to have crocodiles is presented in Appendix 1.

Since the survey by Godshalk in the mid-1970's, two aerial surveys have been conducted on small, isolated, and previously unknown crocodile populations. Although the presence of crocodiles in the Rio Caura had been reported by informants in Godshalk (1978), not much faith was placed in these reports due to the hydrological and limnological nature of the river. The Caura is a medium-large, blackwater river that drains a large section of the Guayanan shield region of Bolivar state. The middle and upper sections of the rivers are very rocky, and the combination of these characters seemed to obviate the likelihood of finding a crocodile population. Nevertheless, during an ichthyological survey of the river in 1981, crocodiles were spotted in the river by R. Franz and S. Reid. The following year they returned to the river to conduct aerial surveys. While the authors did not estimate the total crocodile population in the river, they saw an absolute minimum of 9 large crocodiles, and believed a sizeable population existed in the river. Crocodiles were found primarily in the river section between Maripa, and the falls at Salto Para (115 km), which forms a natural barrier blocking further upstream travel by crocodiles (Franz et al 1985).

In December 1982, aerial surveys of the recently discovered crocodile population in the Rio Tucupido (Portuguesa State) were conducted by Ramo and Busto (1986). The Tucupido is another unusual river for crocodiles and hence crocodiles remained unknown in the area until 1980. The discovery was quite unexpected because the Tucupido is a small, quite shallow piedmont river that runs through the foothills of the Andes not far from the town of Guanare. A total of 5 aerial surveys revealed a range of 5-16 crocodiles, suggesting a small, but potentially viable crocodile population. Crocodile populations in both the Caura and Tucupido are severely threatened by human encroachment (see section 5).

3.4. PRESENT STATUS AND DISTRIBUTION

3.41. Introduction

Beginning in 1985, through the sponsorship of FUDENA, Wildlife Conservation International (New York Zoological Society), WWF, and Tomas Blohm, investigations were initiated to determine the present status and ecology of remaining Orinoco crocodile population in Venezuela. This project developed out of the joint concern of FUDENA and Sr. Blohm for the future survival of the species, and the urgent need to begin a research project to address the conservation needs of the crocodile in Venezuela. The objectives of the the study were threefold: 1) determine the present status of Orinoco crocodiles in Venezuela, 2) investigate conservation-related aspects of the ecology of the species in the wild and under captive conditions, and 3) develop recommendations for a comprehensive conservation program. The research center is located on Hato Masaguaral, a cattle ranch owned and operated by Tomas Blohm in Guarico State. Hato Masaguaral is also the site (since 1984) of a captive breeding and rearing center for Orinoco crocodiles

This report summarizes work completed during the period January 1985-June 1987. Some additional work was done during the wet seasons (June-November), but the accounts of status and ecology presented here primarily come from dry season research. Survey work and ecological studies were restricted primarily to the states of Apure, Guarico and Bolivar, with some additional work in Cojedes and Portuguesa states.

3.42. Methods

Several methods were used to compile information on crocodile status and distribution. Due to limitations of time, and the large area involved, detailed site-specific censusing was only feasible in a few areas. The principal methodologies utilized were: 1) interviews with llanos residents familiar with the llanos fauna, 2) on-site visits to areas and interviews with campesinos, 3) daytime boat or foot surveys of habitat, 4) nocturnal spotlight censuses from boat or shore, and 5) aerial surveys. Most initial information was obtained from literature references or interviews with people knowledgeable concerning llanos fauna. Following this, on-site visits were made to promising areas to talk with campesinos. To avoid leading the informants, questions about crocodiles were framed within the context of inquiries about the local fauna in general. If the informant appeared knowledgeable, more specific questions were asked about crocodiles. Experience showed that if crocodiles were present in an area, local residents could give fairly specific accounts about when and where they could be seen. Diurnal boat or foot surveys were useful to examine the habitat, and look for basking animals or their tracks. Actual censusing could only be accomplished during nocturnal spotlight counts from a boat or, where impassable, on foot.

Nocturnal counts were made from a 12 or 14 foot aluminum boat, powered by a 10 horsepower, or a 15 or 25 hp outboard motor, respectively. Characterization of habitat type, and surveys of nesting/basking beaches was done during the day. Nocturnal spotlight censusing was done principally during the dry season, when crocodiles were concentrated in the main river channels, and when most areas of the llanos were accessible by vehicle. In riverine habitats, censusing was done while travelling downstream to reduce motor noise. During surveys, data on _Caiman_ were also collected. At night, crocodilians were spotted by their reflected eyeshine using a 12 volt, 200,000 candle power spotlight, and/or 4 volt headlamps.

Censusing was usually made more difficult by the presence of numerous _Caiman_, locally referred to as babas. To distinguish crocodiles from babas it was necessary to approach each individual, usually within 5 meters. Crocodiles were recognizable on the basis of size (maximum baba length 2.5 m), or head morphology. Behavioral characters also provided clues to the specific identity of observed crocodilians. Crocodiles were frequently found in open water, away from the shoreline, and were usually much more wary than babas. A typical crocodile would have only the eyes and tip of the snout barely above the surface of the water, and larger individuals would commonly submerge when the boat was still more than 25 m away. Babas frequently held their heads well out of the water, usually allowed a close (<5 m) approach of the boat, and were rarely sighted in open water away from the shore.

When an observed crocodilian could not be definitely identified as a crocodile or baba, they were placed in one of two categories: EO-"eyes only", specific identity unknown but most probably a baba, and EO/C-"eyes only/crocodile", when with reasonable certainty (based on the above behavioral characters) the observed crocodilian was a crocodile.

Large-scale censusing of rivers and reservoirs was done by means of a light fixed-wing aircraft. Aerial surveys were flown during the dry season of 1986 (18-22 April, total 42 hours flying time) and 1987 (13,31 March, 1, 14-17 April, total 47 hours flying time) over areas known to, or suspected to have crocodile populations. The 1986 surveys were flown in a Cessna 170-B, and in 1987 using a Cessna 172 or 206. Flight speeds were 150-170 km/hr, and surveys were flown at an altitude of 150-200 m. Crocodiles were usually spotted basking on shore, although some were seen in shallow water, or floating in open water. Thus surveys were timed for the peak basking periods of the crocodiles (0800-1000 h, 1500-1700 h), although in some cases censuses were extended until 1100 h, or began at 1315 h. Two spotters were present during all surveys. The locations of all crocodiles was noted along with an estimate of total length, notes on habitat, as well as other species of importance (_Caiman_, dolphins and otters). The majority of areas surveys by airplane were chosen based on the likelihood of having crocodiles, and so represent some of the best areas remaining in Venezuela. As with the nocturnal spotlight counts, crocodiles were distinguished from _Caiman_ based on general body and skull morphology, color, and size. Additional information on crocodile distribution in Venezuela was obtained during aerial surveys for West Indian Manatees (_Trichechus manatus_)(O'Shea et al. 1986). Surveys were flown over the middle Orinoco and its

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The results of this survey definitively showed that Orinoco crocodiles are extremely rare in Venezuela. A total of only 273 adult crocodiles were located in the survey area (based primarily on a tally of crocodiles known to riverside dwelling campesinos). Even more alarming, Godshalk reported little evidence of reproduction or recruitment of immature crocodiles into the already greatly reduced populations. One notably positive result of the survey was the discovery of a relatively large, previously unknown crocodile population in the Rio Cojedes. Based on these survey results, Godshalk estimated that the adult crocodile population in Venezuela was approximately 1,000 (IUCN 1983). A list of rivers and caños (small rivers) reported to have crocodiles is presented in Appendix 1.

Since the survey by Godshalk in the mid-1970's, two aerial surveys have been conducted on small, isolated, and previously unknown crocodile populations. Although the presence of crocodiles in the Rio Caura had been reported by informants in Godshalk (1978), not much faith was placed in these reports due to the hydrological and limnological nature of the river. The Caura is a medium-large, blackwater river that drains a large section of the Guayanan shield region of Bolivar state. The middle and upper sections of the rivers are very rocky, and the combination of these characters seemed to obviate the likelihood of finding a crocodile population. Nevertheless, during an ichthyological survey of the river in 1981, crocodiles were spotted in the river by R. Franz and S. Reid. The following year they returned to the river to conduct aerial surveys. While the authors did not estimate the total crocodile population in the river, they saw an absolute minimum of 9 large crocodiles, and believed a sizeable population existed in the river. Crocodiles were found primarily in the river section between Maripa, and the falls at Salto Para (115 km), which forms a natural barrier blocking further upstream travel by crocodiles (Franz et al 1985).

In December 1982, aerial surveys of the recently discovered crocodile population in the Rio Tucupido (Portuguesa State) were conducted by Ramo and Busto (1986). The Tucupido is another unusual river for crocodiles and hence crocodiles remained unknown in the area until 1980. The discovery was quite unexpected because the Tucupido is a small, quite shallow piedmont river that runs through the foothills of the Andes not far from the town of Guanare. A total of 5 aerial surveys revealed a range of 5-16 crocodiles, suggesting a small, but potentially viable crocodile population. Crocodile populations in both the Caura and Tucupido are severely threatened by human encroachment (see section 5).

Beginning in 1985, through the sponsorship of FUDENA, Wildlife Conservation International (New York Zoological Society), WWF, and Tomas Blohm, investigations were initiated to determine the present status and ecology of remaining Orinoco crocodile population in Venezuela. This project developed out of the joint concern of FUDENA and Sr. Blohm for the future survival of the species, and the urgent need to begin a research project to address the conservation needs of the crocodile in Venezuela. The objectives of the the study were threefold: 1) determine the present status of Orinoco crocodiles in Venezuela, 2) investigate conservation-related aspects of the ecology of the species in the wild and under captive conditions, and 3) develop recommendations for a comprehensive conservation program. The research center is located on Hato Masaguaral, a cattle ranch owned and operated by Tomas Blohm in Guarico State. Hato Masaguaral is also the site (since 1984) of a captive breeding and rearing center for Orinoco crocodiles

This report summarizes work completed during the period January 1985-June 1987. Some additional work was done during the wet seasons (June-November), but the accounts of status and ecology presented here primarily come from dry season research. Survey work and ecological studies were restricted primarily to the states of Apure, Guarico and Bolivar, with some additional work in Cojedes and Portuguesa states.

3.42. Methods

Several methods were used to compile information on crocodile status and distribution. Due to limitations of time, and the large area involved, detailed site-specific censusing was only feasible in a few areas. The principal methodologies utilized were: 1) interviews with llanos residents familiar with the llanos fauna, 2) on-site visits to areas and interviews with campesinos, 3) daytime boat or foot surveys of habitat, 4) nocturnal spotlight censuses from boat or shore, and 5) aerial surveys. Most initial information was obtained from literature references or interviews with people knowledgeable concerning llanos fauna. Following this, on-site visits were made to promising areas to talk with campesinos. To avoid leading the informants, questions about crocodiles were framed within the context of inquiries about the local fauna in general. If the informant appeared knowledgeable, more specific questions were asked about crocodiles. Experience showed that if crocodiles were present in an area, local residents could give fairly specific accounts about when and where they could be seen. Diurnal boat or foot surveys were useful to examine the habitat, and look for basking animals or their tracks. Actual censusing could only be accomplished during nocturnal spotlight counts from a boat or, where impassable, on foot.

...basking beaches was d
spotlight censusing was done
crocodiles were concentrated
most areas of the llanos were
habitats, censusing was done
motor noise. During surveys,
night, crocodilians were spott
12 volt, 200,000 candle power

Censusing was usually made
numerous _Caiman_, locally refer
crocodiles from babas it was n
usually within 5 meters. Croc
of size (maximum baba length 2
characters also provided clues
crocodilians. Crocodiles were
from the shoreline, and were u
typical crocodile would have o
barely above the surface of the
commonly submerge when the boat
frequently held their heads wel
close (<5 m) approach of the bo
water away from the shore.

When an observed crocodilian
a crocodile or baba, they were
"eyes only", specific identity
EO/C-"eyes only/crocodile", whe
the above behavioral characters
crocodile.

Large-scale censusing of riv
of a light fixed-wing aircraft.
dry season of 1986 (18-22 April
(13,31 March, 1, 14-17 April, t
known to, or suspected to have
surveys were flown in a Cessna
or 206. Flight speeds were 150-
an altitude of 150-200 m. Croc
shore, although some were seen i
water. Thus surveys were timed
crocodiles (0800-1000 h, 1500-17
censuses were extended until 110
spotters were present during all
crocodiles was noted along with
habitat, as well as other specie
otters). The majority of areas
on the likelihood of having croc
best areas remaining in Venezuel
counts, crocodiles were distingu
body and skull morphology, color
crocodile distribution in Venezue

tributaries (31 hours) and the Orinoco delta (18 hours). Manatee surveys were less intense in their search for crocodiles, but the crocodile sightings provided important supplementary information on crocodiles in several areas (Thorbjarnarson et al., in press). Appendix 2 lists all aerial survey flights for crocodiles 1987-8, and the manatee survey flights in 1986.

3.43 Results

3.431 Rio Orinoco

The river from whence C. intermedius gets its common name is at present essentially devoid of crocodiles. The Orinoco was one of the first areas hunted out by the caimaneros during the 1930's, and little or no population recovery has taken place. The river is heavily utilized as a transportation route, and most of the riverbanks and major mid-channel islands are settled or used for agriculture. Continued hunting or incidental mortality has effectively kept crocodile populations low. Aerial surveys for crocodiles in 1986 (560 km of river), and 1987 (45 km) found no crocodiles (Table 2). However, during aerial surveys for manatees in March 1986, crocodiles were sighted basking in two separate locations: near La Sardinia (Edo. Anzoategui, 7 adult crocodiles on two adjacent mid-channel islands), and just west of Borbon (Edo. Bolivar, two crocodiles on south river bank)(O'Shea et al. 1986).

Comments received during interviews also suggest a dearth of crocodiles in the Orinoco. However, certain sections of the river were said to still have small populations. Among these were the region between the mouths of the Rios Apure and the Arauca, especially near Isla Cabure, and in the vicinity of Las Bonitas (Edo. Bolivar). Crocodiles are also still seen occasionally in the Orinoco near Puerto Ayacucho (Amazonas Terr.). Two captive crocodiles in Puerto Ayacucho (FONAIP station) and one in San Fernando de Apure are reportedly from the Puerto Ayacucho region. Additionally, a 4 meter crocodile was captured alive in a fishing net (and later sold) in the Orinoco near the mouth of the Rio Parguaza in June 1986 (pers. obs.). These data suggest that crocodiles may still be found at very low densities in many parts of the river.

3.432 Apure State

Apure state (76,500 sq. km) is centrally located in the low-lying western llanos region, and is bounded by the Rio's Apure, Orinoco, and Meta. Most of the state is still sparsely inhabited (mean density 2.2/sq. km), with the majority of the population located along the Rio Apure . Crocodiles were seen, or reported from a number of rivers in this state, however, usually in very low numbers. Crocodiles are even reported to be seen on occasion in some of the Eichornia covered caños and canals not far from the capital of San Fernando. However, by far the most important crocodile population remaining in Apure, and one of the largest remaining anywhere, is in the Rio Capanaparo. The following section presents survey data for the Rio Capanaparo, then the other Apure rivers.

a. Rio Capanaparo

Aerial Surveys--The Capanaparo is a medium size, turbid water river that runs over the nutrient poor llanos region south of the Rio Arauca. A thin strip of gallery forest borders the river and its many associated oxbow lakes. Aerial surveys in 1986 and 1987 revealed a relatively healthy crocodile population upstream of Macanilla, and downstream of the Rio Riecito (188 km). The Capanaparo provided nearly ideal conditions for performing aerial surveys. The river was broad enough to allow one observer on each side to cover virtually all potential basking beaches. The river did not have extreme meanders, nor heavy overhanging forest cover, and perhaps most importantly, the virtual absence of boat traffic meant that a sizeable portion of the crocodile population could be expected to be out basking during the mid-morning hours 0800-1000 h. Small crocodilians were difficult to spot from the airplane, and no crocodiles less than 1.0 m total length were observed.

Mean observed densities were approximately 0.1 crocodiles/km, or one crocodile for every 10 kilometers of river. However, the upstream section above the Rio Riecito, and the lower 90 km adjacent the Rio Orinoco had much lower crocodile densities, and excluding these sections density figures almost doubled (0.174-0.218/km).

During 1986, 445 km of the Capanaparo was flown once (Caño Cubarro to the Rio Orinoco, Table 3). A total of 39 crocodiles were seen, for an overall uncorrected density of 0.088/km (Table 3). Highest crocodile densities were noted in sections between Sta Rosa-San Pablo (0.143/km), and San Pablo-Sta Ana (0.300/km).

During April of 1987, sections of the Rio Capanaparo were surveyed on 4 separate days (1, 14, 16, 17 April). Surveys did not extend above the Rio Riecito. To facilitate data analysis, the portion of the Capanaparo surveyed was divided into 10 sections (Table 4) ranging from 12 to 53 km in length. The number of crocodiles observed was tabulated for each section, and density calculated. Most sections were surveyed two times, and three sections were surveyed on three separate occasions.

On any one survey only an unknown fraction of the crocodile population (over 1.0 m) was observed. Repetitive censusing allowed crude correction factors to be applied to better estimate the true number of crocodiles in each river section. Initially, three correction factors were applied to estimate true population size: 1) the maximum number of crocodiles seen on any one aerial survey, 2) correction for size-class, and 3) correction for size-class and location.

The first method simply used the maximum number of crocodiles seen in any one river section as the best estimate of population size. Correction for size-class involved dividing observed crocodiles into 4 size-classes (1-2, 2-3, 3-4, and 4+ meters total length). The maximum number of crocodiles, per size-class, per river section was summed to provide a total count. Correction 3 went one step further and divided crocodiles by size, and position within the survey section. If two crocodiles were in the same size-class, but seen x or more kilometers apart during separate surveys, they were considered to be different crocodiles. The value of x was arbitrarily set at 2 kilometers.

Table 5 summarizes the crocodile densities obtained using the three correction methods. As in 1986, no crocodiles were seen in the section nearest the confluence with the Rio Orinoco. The 1987 data show a peak crocodile density in section 3 (Caño Amarillo-San Luis, 25 km), with an estimated 1.8 crocodiles per kilometer. These data differ from the 1986 census, which found a peak further downstream (corresponding to sections 8-9 of 1987). This difference presumably results from a difference in time of day when the river was surveyed. In the 1986 census, the upstream sections of the Capanaparo were flown during the afternoon. The afternoon basking peak is usually smaller than the morning peak, so a smaller fraction of the crocodile population is visible during the afternoon hours. The downstream sections in 1986 were flown the following morning, during the morning basking peak and resulted in a greater density in these river sections. In part this, may also explain the absence of crocodiles from the upstream section of the Capanaparo during the 1986 survey, as this section was flown during the early afternoon (1322-1435 h) when few crocodiles would be visible. A comparison of river sections 2-7 flown during the afternoon hours in 1986, and during the morning in 1987, suggests that approximately half again as many crocodiles may be out basking during the morning hours (1986 count x 1.58=1987 total). Thus, the true distribution of crocodiles in the Capanaparo is more closely reflected by the 1987 results, where repetitive surveys were flown entirely during the morning hours.

However, based on the results of nocturnal spotlight counts in section 3, it was felt that even using the largest population estimate from the aerial surveys (correction 3), crocodile populations were still being underestimated. To more accurately determine crocodile population size, an estimate was made of the probability (P) of spotting crocodiles during an average aerial survey. Because most sections were censused only two or three times, the calculation of this sighting fraction only provides a rough estimate of P. Furthermore, a comparison of crocodile size-class distributions obtained from nocturnal spotlight counts and aerial surveys for river section 3 indicated that the value of P is smaller for 1-2 meter crocodiles than it is for larger individuals. Hence, two values of P were calculated, one for 1-2 m crocodiles P_{1-2}) and one for larger crocodiles ($P_{>2}$)(see Appendix 3). The estimated sighting fractions were 0.27 for crocodiles over 2 meters, and 0.12 for 1-2 m crocodiles. Using these values, more realistic estimates of non-juvenile population size were obtained.

Aerial surveys provided an expedient method for quickly surveying a major portion of the river. However, as only crocodiles over 1.0 m long were spotted, a major segment of the population could not be counted. In order to census juvenile crocodiles, as well as gather important ecological data, two nocturnal spotlight censuses of section 3 were conducted (Table 7). These data were combined with aerial survey data to estimate the total crocodile population in the Rio Capanaparo downstream from the Rio Riecito.

For each river section, the number of non-hatchling crocodiles was estimated using the formula:

$$N_x = [(M_{>2}/P_{>2})+(M_{1-2}/P_{1-2})]/F_{>1}$$

where: N_x = estimated non-hatchling population in river section x;
$M_{>2}$ = mean number of crocodiles greater than 2m TL observed in section x during aerial surveys.
M_{1-2}= mean number of 1-2 m TL crocodiles seen in river section x
$F_{>1}$ = fraction of crocodile population >1.0 m total length (0.25)
$P_{>2}$ = probability of seeing any one crocodile greater than 2 m TL during an average aerial survey (0.27)
P_{1-2}= probability of seeing a 1-2 m TL crocodile during aerial surveys (0.12).

The results of these population estimates are presented by river section in Table 8. Based on these data the total estimated non-hatchling population for the Rio Capanaparo below the Rio Riecito is 233, of which 102 (43.9%) are found within the 25 km long section 3.

Nocturnal Surveys--Nocturnal spotlight counts were conducted in river section 3 during February and April 1987. Total uncorrected population density was 1.64/km (total 41 non-hatchlings observed). The two surveys were inadequate for estimating the sighting fraction (P), so published values for *Crocodylus porosus* from Australia were utilized (Bayliss et al. 1986). These values are size-class specific and resulted in a total non-hatchling population estimate of 114 (4.56/km) for river section 3 (Table 9). This value is slightly higher, but in general agreement with the figure estimated using aerial survey data.

Total Population Estimate: Rio Capanaparo Basin--To estimate the non-hatchling crocodile population in the Capanaparo basin in Venezuela requires an approximation of the crocodile population in areas that were not covered in the aerial survey. These areas may be split into 4 categories: 1) the Rio Capanaparo upstream of the Rio Riecito, 2) the Rio Riecito, 3) oxbow lakes associated with the Capanaparo, and 4) tributary caños of the Capanaparo (other than the Riecito).

Above the Rio Riecito, the Capanaparo runs for another 190 km within Venezuelan territory. Although 157 km of this was surveyed in 1986 and no crocodiles were seen, this survey was done during an unfavorable time of the day (1322-1435 h) when few crocodiles are visible from a fixed-wing aircraft. Crocodiles are known from the Capanaparo in Colombia (Medem 1981), so it is reasonable to assume they are also found in the upstream sections in Venezuela. The estimated non-hatchling crocodile density in the furthest upstream section surveyed in 1987 (section 1) was 0.39/km. Assuming a mean density of 0.4/km upstream of this point, we can estimate 190 km x 0.40 crocodiles/km= 76 non-hatchling crocodiles.

In 1987, approximately 84 km of the Rio Riecito was censused by fixed wing aircraft during the afternoon of 16 April. The observed crocodile density was 0.023 crocodiles per kilometer, and the total length of the main river course in Venezuela estimated at 250 km. To better estimate non-hatchling crocodile density three correction factors were used: 1) morning counts reveal 1.58 times as many crocodiles as afternoon counts (see above), and 2) morning counts reveal approximately 27% of the crocodiles over 2.0 m total length, and 3) 52.8% of the population is below 2.0 m. Using these correction factors, the non-hatchling crocodile population density was estimated to be 0.28/km, and the total population size approximately 71.

The amount of oxbow lake habitat in the Rio Capanaparo below the Rio Riecito was estimated from 1:100,000 scale maps. Only relatively new oxbows or caño entrances were used in this analysis as it was noted that old, overgrown oxbows were rarely used by crocodiles (Section 4.12). Nocturnal spotlight counts in section 3 revealed a density of 1.45 crocodiles/straight line km in 4 oxbow lakes (8 crocodiles/5.5 km). It was felt that this density was unusually high because it included two very recent oxbows formed within the last 25 years. These two oxbows were the only ones to have crocodiles, the other 2, more typical oxbows, had no crocodiles. Hence, to better estimate crocodile density in oxbows, a value of one half the crocodile density in the adjacent river section was used. A total of 23 non-hatchling crocodiles was calculated in 42 km of recent oxbow lakes.

The last segment of the crocodile population in the Capanaparo basin to be estimated is that of the caño tributaries. In this analysis only the major caños were included: Quitaparo (100 km), Naure (40 km), Casanarito (80 km), La Pica (100 km), and La Guardia (75 km). Interviews with local residents suggested that all these, and other caños, contained crocodiles. As the density of crocodiles was unknown, an arbitrary, conservative figure of 0.1/km was chosen. The resulting non-hatchling population estimate was 40.

The sum total of these population estimates for the entire Capanaparo basin in Venezuela is 443 non-hatchling crocodiles (Table 10). Many of these figures are, of necessity, conservative, but this analysis suggests that probably no more than 500 non-hatchling crocodiles exist in the Venezuelan portion of the Capanaparo basin today.

b. Rio Cinaruco. The Cinaruco is a shallow, very sandy, clear water river that, along with the Capanaparo, drains a large section of the nutrient poor savanna region between the Rios Meta and the Arauca. However, unlike the Capanaparo, the Cinaruco receives little drainage from the Andean foothills to the west, hence it has a low sediment load and is a very clear, nutrient poor river. The region is very sparsely populated, with mostly Indian settlements along the upper and middle sections, and little or no boat traffic during the dry season. The Cinaruco was flown twice, once in 1986, and again in 1987. Both surveys were conducted in the afternoon (Appendix 2). Crocodiles were only seen during the 1986 survey, when two adults were spotted in the water at a point just upstream of the entrance of the Caño Caga Ligero (approximately 280 km upstream from the mouth). The 1987 survey was terminated before it reached the point where crocodiles were seen the previous year. The upper section of the river where the crocodiles were seen differs significantly from the downstream portion, with more frequent deepwater pools (termed "charcos") of slow moving water, and almost no sandy, shallow water segments.

Comments by residents of Campamento Mobil, located approximately 50 km upstream from the Orinoco suggest that a diffuse crocodile population also exists in the downstream region of the Cinaruco. Crocodiles were also reported to be found in clear water affluents such as the Rio Juriepe, and the Caño Potrerito. Godshalk (1978) came to the same conclusion during his survey of the Cinaruco.

c. Rio Claro. The Rio Claro is a small, clearwater tributary of the Rio Cunavichito, draining into the maze of waterways near the Orinoco between the Rio Arauca and the Capanaparo. The Rio Claro runs over sandy, nutrient poor soils, and dries up into a series of charcos during the dry season. These charcos may be interconnected by small streams, or remain completely isolated. Much of the land around the river is privately owned by individuals who limit access to the river. A brief aerial survey of the river revealed no crocodiles, but according to local campesinos the river contains crocodiles that dig burrows and remain hidden during most of the dry season.

d. Rio Arauca. The Rio Arauca is a medium size, turbid water river draining the extensive, low-lying region between the Rio Apure and the Capanaparo. Aerial surveys of the middle and upper sections in Venezuela were flown in 1986, and a short section near the mouth in 1987 (Table 2). The region surrounding the river is settled in many parts, and the river itself is used extensively for transport both during the dry and the wet seasons.

In 1986 the area surveyed extended 335 km upstream from Paso Arauca, to the vicinity of the Caño Santa Clara. A dense *Caiman* population was found but no crocodiles were seen. In 1987 only 9 km upstream from the mouth were flown. One crocodile was seen in the water adjacent to a steep embankment.

Crocodiles are still seen periodically by residents along the river, but the population is very disperse. Because of its heavy human usage, the few remaining crocodiles are very wary and not easily seen.

3.433 Portuguesa State

One river in Portuguesa state was surveyed, the Rio Tucupido. The Tucupido crocodile population was unknown to science until 1980, when crocodiles were discovered there accidentally. The Tucupido is poor crocodile habitat in the classical sense, being a small piedmont river draining the foothills of the Andes just to the northwest of Guanare, the capital of Portuguesa state. However, a small but locally dense crocodile population (Ramo and Busto 1986) has managed to survive there, principally because the region has remained very isolated until recently.

Two aerial surveys were flown over the Tucupido on consecutive days in 1986 (Table 2). The maximum number of crocodiles spotted was 19, which over a survey length of 31 kilometers represents a density of 0.613 crocodiles/km, the highest aerial survey density found during this study. Eight days after the aerial survey, a nocturnal census of 7.2 km of river revealed a density of 1.34 juvenile crocodiles per km. Assuming a 40% sighting fraction for aerial surveys, and a 70% sighting fraction for juvenile crocodiles on nocturnal spotlight counts (Messel et al. 1981, Bayliss et al. 1986), the estimated crocodile density in the Tucupido is adults/subadults- 0.613/0.40=1.53, juveniles- 1.34/0.70= 1.91, or a combined density of 3.44 non-hatchling crocodiles/km. This would suggest a total non-hatchling population of 107 crocodiles in the 31 kilometers above the dam construction site where the aerial surveys began.

Extensive sandy beaches are present and provide good nesting habitat. One recently opened nest was found, and a total of 14 hatchlings counted in the river next to an attending adult .

A number of crocodiles have been killed in the Tucupido during the last several years. Because the river level drops sharply during the dry season, crocodiles in the Tucupido dig burrows into the river bank, and become vulnerable to hunters who will pull them out of these dens. Currently, a dam is being constructed along the Tucupido that will flood that part of the river where the crocodiles are found. The nearby Rio Bocono was recently dammed, and the two rivers will form one reservoir. The drastic change in habitat will effectively remove sandy nesting beaches, and force crocodiles to live in a lacustrine habitat, where potential competition with Caiman may be more intense (see Section 4.4 Ecological Interactions). On the other hand, living in a more permanent, deep water habitat will make the crocodiles less vulnerable to poachers.

The Rio Cojedes/Sarare system found in neighboring Cojedes state and partially in Portuguesa state contains one of the largest remaining Orinoco crocodile populations in existence. Although it is found in an area heavily developed for agriculture, and in very polluted river, crocodiles have managed to survive. This crocodile population was first uncovered by Godshalk (1978, 1982), and is currently under investigation by Dr. Jose Ayarzaguena of the La Salle Society. Preliminary results of aerial and nocturnal surveys indicate that at least 150 crocodiles remain in this region (Ayarzaguena 1987).

3.434 Guarico and Aragua States

These two states are located in the north-central llanos region. Aragua state (7,014 sq. km) contains only a small region of llanos habitat along its southern boundary. Guarico state (64,986 sq. km) is located entirely within the llanos region, is one of Venezuela's principal agricultural and cattle rearing regions, and has an overall moderate to low population density (4.9 inhab./sq. km)

a. Rio Guarico. Initial information suggested that crocodiles may be found in at least three parts of the Rio Guarico, two of which were reservoirs (Embalse de Camatagua, Aragua state, Embalse de Guarico, Guarico state). The other "population" was located in the Caño

Rabanal/Caño El Caballo, through which the Rio Guarico now runs because of a change in river course approximately 30 years ago. The Rio Guarico is a small-medium sized turbid water river draining a section of the north-central llanos region and adjacent southern slopes of the coastal mountain range. Water level now varies some 3-4 meters on an annual basis, and an extensive deciduous-mesofil forest fringes the river for much of its course.

Embalse de Camatagua--This reservoir was formed in 1969 by damming the Rio Guarico near Camatagua. The river flooded back into a hilly, piedmont area forming a reservoir principally bordered by steep hillsides, with occasional lower, swampy regions near the entrances of tributary streams. An extensive fringe of semi-floating vegetation (mostly Chara) is found around the lake fringe.

Crocodiles were seen in the Embalse de Camatagua during surveys in 1986 (13 seen) and 1987 (6 seen). Most crocodiles were observed "basking" atop the fringe of floating vegetation, where sunlight would rapidly heat the water. Because habitat conditions were very different from those of the Rio Capanaparo, the derived estimate of the sighting fraction cannot be applied, but almost certainly is significantly smaller. Two nocturnal spotlight counts (10 June, 3 December 1986) along 19 km of shoreline revealed a very high Caiman density, but very few crocodiles (0.05/km, and 0.00/km). One nest site was located, in a steep thalus/soil slope, and 25 hatchlings and one adult crocodile were seen nearby (the only non-hatchling crocodile seen). Although more survey work needs to be done to better estimate population size, the number of non-hatchling crocodiles in the Camatagua reservoir probably numbers more than 50.

Over the last 10 years several crocodiles have been killed both in the reservoir, and in the Rio Guarico just below the dam. Other than sport fishing, the reservoir is not used much. Most of the crocodiles that have been killed were shot by local residents. Several crocodiles have also been killed or taken out of the river below the dam.

Embalse de Guarico--This reservoir was formed in 1957 by the damming of the Rio Guarico at Calabozo. The river flooded a broad expanse of low-lying llanos, creating an enormous, shallow water reservoir. In most areas, dead trees still remain visible, and the shoreline is primarily mudflats or marsh. The south rim of the embalse is heavily populated by some of the barrios around Calabozo, but the northern section forms an extensive marsh, sparsely inhabited, which is an important habitat for many species of waterfowl. Boat traffic is limited to a few fishermen and duck hunters. Crocodiles were reported from this reservoir, and the adjacent inflowing section of the Rio Guarico by a number of local sources. During two aerial surveys, no crocodiles and only a few Caiman were spotted. However, due to the nearly ubiquitous presence of large fallen trees along the lakeshore, the spotting of crocodilians was very difficult. Nevertheless, the few remaining crocodiles are apparently very wary. Little evidence of reproduction is known from this reservoir, although occasional juvenile crocodiles are seen or captured in some of the surrounding irrigation canals and may originate from the embalse.

Caño Rabanal-El Caballo--During the late 1950's, the course of the Rio Guarico downstream from the Embalse de Guarico changed, with the new water course flowing through the Caño Rabanal and Caño El Caballo, and eventually drains into the Rio Guariquito. During the dry season, most boat traffic through these caños is limited by the presence of several rapids or "raudales". In deep water charcos between or just upstream of these raudales is a small crocodile population. During a short aerial survey in 1986, one crocodile was spotted (0.022/km). Day surveys on foot of the Caño Rabanal revealed the presence of two adult crocodiles in one charco, and one 3 meter crocodile was found shot on a riverbank in the same charco in January 1986. Local residents say that crocodiles are frequently seen in other parts of the river, but are very wary and difficult to see. Night surveys by boat and on foot failed to reveal any crocodiles. On 30 July 1986, 38 km of the Caño Rabanal and the adjacent upstream section of the Rio Guarico was surveyed without seeing a crocodile.

Local residents say that reproduction does occur and the remains of a hatched nest was reported from the Rabanal in 1984. Only one juvenile crocodile (1.2 m TL) was seen during day surveys.

Rio Orituco--The Orituco is a small tributary of the Rio Guarico that feeds into the latter river just southeast of Calabozo. The Orituco was noted by Humboldt (1860) for having very aggressive crocodiles. Recent reports indicated that despite the close proximity to a major town, crocodiles were still found in the Orituco. Like many smaller rivers, the Orituco dries up into a series of interconnected, or isolated charcos during the dry season (December-April). One such charco, reported to have crocodiles was surveyed at night on 14 May 1987. Over a total length of 2.3 km, 2 small adult or subadult crocodiles (2-2.5 m TL) were observed. Only three weeks previous to the survey, another crocodile (2.6 m TL, female) had been captured alive and taken from this area. Local residents also say a large crocodile (4-5 m TL) is seen in the same charco.

b. Rio Chirgua. The Rio Chirgua is another small-medium sized, turbid water river that runs through a heavily forested region along the border between Guarico and Cojedes states. The area has been relatively isolated until recently, and wildlife is still fairly abundant in many places. Crocodiles were reported in this river both by personnel from Hato Pinero in Cojedes, and Hato El Tigrillo in Guarico. The river has densely forested banks and so aerial surveys were impractical. Many sections of the river are impassable by boat due to blocking emergent vegetation and tree trunks. However, a number of river sections are navigable for short sections and one such section (approximately 3.5 km long) was surveyed in 1985 and 1986. Although local residents say that crocodiles are seen in this stretch of river, none were observed during the night census.

c. Rio Manapire and Rio Aguaro. Both the Aguaro and the Manapire rivers are located in the llanos of eastern Guarico state. The Aguaro forms the eastern boundary for much of the Aguaro-Guariquito National Park, and is a small, clear water river draining the open palm savanna regions in the eastern section of the park. The

Manapire is a turbid water river that runs through a heavily forested region. Reports indicated that a reproductive population of crocodiles existed in the Manapire, and that people in the nearby town of Santa Rita would dig up and eat the eggs in January and February. During the dry season the river dries up significantly, and remains as a series of disconnected charcos. Under these conditions, crocodiles usually have burrows with underwater entrances and are very difficult to observe. An aerial survey of the 50 km of river upstream from the confluence with the Orinoco (April 1986) revealed no crocodiles. Because the region was so heavily forested and the river meandered extensively, survey conditions were very poor, and little can be based on this census. Further census work needs to be done on this river.

The Rio Aguaro was also censused by airplane (40 km, April 1986), and by nocturnal boat survey (13.5 km, Sept 1986). No crocodiles were seen on either survey. Local residents say crocodiles are seen only rarely in this river. The nearby Rio Guariquito which forms the western boundary of the national park was surveyed by day in September 1986. The Guariquito is a medium-large turbid water river that forms good crocodile habitat. However, it is heavily used as a route of transportation, and for fishing. Local residents indicated that crocodiles are not seen in the part of the Guariquito adjacent the national park.

3.435 Bolivar State

Bolivar state is a large (238,000 sq. km), sparsely inhabited (1.7 inhab./sq. km) region south of the Orinoco river. Habitats range from open savannas along the Orinoco, to dense tropical rain forest. The regions of this state outside the floodplain of the Orinoco river was never considered good crocodile habitat. Nevertheless, crocodile populations have been noted from some rivers.

a. Rio Caura. The Caura is a large blackwater river that drains the western Guyanan shield region of Bolivar state. As mentioned in section 3.3, the presence of crocodiles in the Rio Caura remained unknown to science until the early 1980's. Crocodiles were not thought to inhabit blackwater, nor swift flowing rocky rivers, both of which well characterize the upper and middle sections of the Caura. The Caura was surveyed twice by airplane in 1986, once each during crocodile and manatee surveys. Both surveys observed only 4 crocodiles (0.016/km), all located upstream from the town of Las Trincheras. A dugout canoe trip was made up the Caura 23-27 March 7 1987. Due to the rocky nature of the river, and the presence of numerous rapids, night surveying was difficult. During two nocturnal boat surveys ,covering a total of 6 km of river, only one crocodile was spotted (0.17/km), a 1-1.5 m TL juvenile seen near the base of the Salto Para. These falls form the upstream limit to crocodile distribution on the Caura. An additional 7 km of the Rio Nichare, a clearwater tributary were surveyed at night, but no crocodiles were observed.

b. Rio Cuchivero. The Cuchivero is the next major Orinoco River tributary to the west of the Caura. It is a smaller, clearwater river that courses through some 150 km of savanna before entering the Orinoco. Aerial surveys of the lower 140 km of the Cuchivero failed to reveal any crocodiles. The possible presence of crocodiles in this river, and the Rio Guaniamo (a major Cuchivero tributary) was suggested by Sr. Nouble Seguias of Caicara. Sr. Seguias had one 2.2 m TL female crocodile in captivity that reportedly came from the Cuchivero. The upper regions of the Guaniamo are being extensively mined, and the waste from these operations has discolored the Guaniamo. The lower section of the Cuchivero has a light green color.

Other rivers in Bolivar state may still contain small crocodile populations. The most frequently mentioned, and most likely based on habitat considerations, are the Rio Parguaza, and the Rio Suapure.

3.436. Amazonas Territory.

Amazonas territory is a vast (175,750 sq. km), virtually unpopulated (0.1 inhab./sq.km) region in southernmost Venezuela, bordering on Brazil and Colombia. The territory contains the headwaters of both the Rio Orinoco, and the Rio Negro, a major blackwater Amazon tributary. The two drainages are interconnected by the Brazo Casiquiare. No survey work was done specifically in Amazonas territory. One river, the Rio Ventuari was flown during the manatee survey in 1986, and 2 crocodiles were spotted (O'Shea et al. 1986). The Ventuari is a medium-large clearwater river that drains the northeastern part of the territory. Informants in Puerto Ayacucho stated that crocodiles are still seen in the Rio Orinoco near Pto Ayacucho, and also in the Rio Ventuari. One informant, a boatman for the Ministry of Agriculture (MAC), said crocodiles ("caimanes") are also seen in the Brazo Casiquiare. However, this report remains unconfirmed.

3.437. Delta Amacuro

The only survey work of the Orinoco delta region was 18 hours of aerial surveys flown looking for manatees in 1986. During these surveys, observers were also looking for crocodiles. Most of the major caños within the delta were covered (appendix 2), but no crocodiles were spotted.

4. ECOLOGY OF THE ORINOCO CROCODILE

4.1 HABITAT RELATIONS

4.11 Macrohabitat

4.111 General Features of the Orinoco Basin

The Orinoco crocodile is principally a dweller of freshwater riverine environments of the Orinoco basin, where it is encountered in a wide range of habitats. A discussion of the macrohabitat relations of the Orinoco crocodile must first treat the diversity of aquatic environments within the range of the crocodile. Although its range extends into the evergreen forested regions of Bolivar state and Territorio Federal Amazonas, the Orinoco crocodile was historically most abundant in the llanos region of Colombia and Venezuela. The llanos is a large (252,530 km^2) geosyncline located between the Coastal range to the north, and the Andes to the west, and the Guayanan shield region to the south. This region is best described as a hyper-seasonal savanna intermixed with varying amounts deciduous or semideciduous forest. The entire area is drained by the Orinoco river, and tributaries cross the llanos principally in a north-south, or west-east direction. Situated over pre-Cambrian basement rocks, the llanos is composed primarily of alluvial deposits from the Tertiary and Quaternary periods. Most surface sediments are quite recent, associated with the Pleistocene uplift of the llanos region, and erosional deposition from the Andes and coastal range.

According to Sarmiento (1983) the llanos can be divided into four basic subregions: the piedmont region adjacent to the Andes, the high plains, the alluvial overflow region, and the aeolian plains. Mountainous foothills, fast flowing rocky rivers and streams, and large alluvial fans characterize the piedmont region. Vegetation is principally savanna, with varying amounts of semi-deciduous tropical forest. This subregion is principally located along the base of the Andes and Coastal mountain ranges. The high plains, or upper llanos region are also characterized by a relatively significant amount of vertical relief, here dominated by mesas with dissected or undulating topography. Pittier (1942) first described this region as one of low plateaus 200-300 m above sea level, crossed by Orinoco tributaries carving deep river courses. This subregion is divided between two principal areas, the eastern llanos of Monagas, Anzoategui, northern Bolivar, and eastern Guarico states, and the llanos region south of the Rio Meta in Colombia. These two units are separated by a central tectonic depression (occupied by alluvial plains), and may be remnants of a formerly continuous uplands region from the Pliocene-early Pleistocene. The typical tree savanna vegetation is dominated almost exclusively by three species: Bowdichia virgiloides, Byrsonomia crassifolia, and Curatella americana (Sarmiento 1983).

The alluvial overflow plain, or lower llanos is a vast region almost without vertical relief that occupies a depression in the central part of the llanos. The dominant vegetational association in this region is the hyperseasonal savanna, characterized by few trees or palm (Copernicia tectorum) savannas (Sarmiento 1983). In the wet season, the rivers in this region generally overflow, and most areas flood from this and heavy rainfall combined with poor surface drainage and soils of poor permeability. The western and more northern sections of this subregion are characterized by more dense semideciduous forest cover.

The aeolian plains regions of the llanos extends from the upper Meta region in Colombia to the northeast, including the Cinaruco and Capanaparo river drainages, and apparently is a remnant of the formerly arid climatic period during the Wurm glaciation (Tricart 1974). This region contains extensive dune fields oriented in a northeast-southwest direction, situated atop sandy soils. Vegetation is characterized by open, virtually treeless savannas, with thin strips of gallery forest or small palm-lined morichales (small streams lined with moriche palm, Mauritia minor).

The entire llanos region is climatically hyperseasonal with a well defined wet season (May-November) during which over 75% of the rainfall occurs. Total annual rainfall in the llanos region generally ranges from 1000-2000 mm, with rainfall increasing towards the west and south. A mean annual temperature of 26-28 C., results in a Tropical Dry Forest plant association, as defined by the Holdridge system (Ewel and Madriz 1968).

The rest of the range of the Orinoco crocodile can be conveniently lumped into the Guayanan region, including the Territorios Federales Delta Amacuro and Amazonas, and Bolivar state. Although this region contains an appreciable amount of savanna habitat, 82% is covered by forest, representing some 42% of the Venezuela's forest (MARNR 1982). An estimated 80% of the country's surface water originates from this area. The Orinoco delta is a large (42,200 km²) region of mangroves, palm savannas, and large river channels or caños.

4.112 Diversity of Aquatic Habitats.

Although during the wet season much of the lower llanos becomes flooded and provides potential habitat, crocodiles are restricted principally to the rivers and their immediate floodplain. Hence the following discussion will center on riverine habitats and crocodile distribution.

The Orinoco river is one of the South American continent's largest river systems. Originating in southern Venezuela near the Brazilian border, the Orinoco travels 2,060 km and drains a total 880,000 km² before entering the Atlantic through its delta. Due to a marked seasonality in rainfall throughout much of the basin, the Orinoco, and the vast majority of its tributaries undergo a significant annual change in flow. In the lower Orinoco at Musinacio, river level varies some 13 meters, and flow rate can change as much as 10 fold during the year (MOP 1972) (Appendix 4).

Orinoco tributaries can be divided into 2 major categories and 4 types:

- I. Llanos tributaries
  - a. Andean/Coastal Range drainage
  - b. Internal Llanos drainage
- II. Guayanan tributaries
  - a. Blackwater rivers
  - b. Clearwater rivers

Among the type I tributaries, the Andean/Coastal Range rivers are the largest, and contain a high sediment load. These tributaries, (e.g. Rio Apure, Arauca) as well as the Orinoco itself, provided optimal crocodile habitat. The smaller internal llanos drainage systems (e.g. Cinaruco, Vichada) are usually clearwater systems with lower overall biological productivity (Appendix 4). Crocodiles are or have been reported from these drainages, but apparently in lower densities. One of the largest remaining crocodile populations, that of the Rio Capanaparo, is found in a river intermediate between these two types.

The Guayanan tributaries (type II) may be blackwater (e.g. Rio Caroni), or clearwater (e.g. Rio Suapure). Various clearwater rivers have been reported to have low crocodile densities (Cuchivero, Ventuari). The only true large blackwater tributary in the lower or middle Orinoco is the Caroni, and historically it has been noted for its absence of crocodiles. The Rio Caura, which has characteristics of both clear and blackwater, has a small crocodile population (section 3.4).

Type Ia rivers are by far the most common Orinoco tributaries in the llanos ecosystem. As they receive a significant amount of drainage from the Andean or Coastal mountain range, they are usually large tributaries. This is especially true of the Andean rivers such as the Apure (principally Andean drainage), and the Meta and the Arauca (completely Andean). Rivers that drain the Coastal Range are smaller in size and more seasonal in nature, the two largest independent systems are the Guarico, and the Manapire. In the eastern llanos of Anzoategui and Monagas, the Orinoco tributaries are normally small, and drain the high llanos mesa regions in the northern parts of these states.

Within the type Ia Orinoco tributaries, the rivers can be divided into 3 subsections: 1) mountain/piedmont, 2) upper llanos, and 3) the lower llanos section.

The mountain/piedmont river sections represent the headwaters of these Orinoco tributaries and are generally small in size, swift and rocky. Many of these rivers, especially in the Andes region, flow though steep, narrow valleys filled with what was formerly dense evergreen forest. In the upper llanos regions, these rivers run through recent alluvial deposition and ordinarily are contained within the river course by high banks, limiting flooding of surrounding regions during the wet season. Rivers in the upper llanos normally have an associated gallery forest, or flow though more extensive semi-deciduous forests, and begin to take on a meandering aspect. In some of the llanos rivers, this meandering is accentuated as the rivers enter the lower llanos, where rainy season floods frequently cause the rivers to overflow. In this area rivers commonly bifurcate downstream, often forming complicated delta-like drainages.

Although historically, the lower llanos region of type Ia rivers provided optimal crocodile habitat, crocodiles were, and still are, found in all of these subsections. For example the present Tucupido river population is in a piedmont region, and the Cojedes-Sarare crocodile population in upper llanos. Due to intense hunting pressure and the long-term negative effects of human populations on wildlife populations, no large, locally dense crocodile populations remain in what was formerly the most optimal type of habitat available; the low llanos sections of type Ia rivers. Hence, much of the following discussion of habitat relations and other aspects of ecology may be somewhat biased, as it is based on remnant populations located outside of the formerly optimal habitat.

Historical accounts and information from hide dealers suggest that crocodiles were most abundant in the Orinoco, and in low llanos sections of type Ia tributary systems. In Venezuela, rivers such as the Orinoco, Apure, Portuguesa, Guarico, Arauca, and Capanaparo were mentioned as the source of the majority of the skins traded during the period 1930-1950 (Medem 1983). The corresponding rivers in Colombia were the Meta and the Guaviare-Guayabero (Medem 1981). Crocodiles from type Ib rivers were also hunted (Rios Cinaruco and Cuchivero in Venezuela, Rio Vichada in Colombia), but in these areas were reported much less common (e.g. Rio Vichada system according to Medem (1981) only supplied 200 hides during the period of commercial exploitation). Other type Ib Orinoco tributaries in Colombia such as the Tuparro, Tomo and Bita were reported to only contain small numbers of crocodiles in the 1940's (Medem 1974).

Little or no hunting has been reported from type IIb tributaries, with the exception of the Rio Caura, where caimaneros apparently began working long after most other regions had been hunted out (1960's).

The preference of crocodiles for type Ia rivers is perhaps best understood by considering reasons why crocodiles are less abundant in the other river types. Type Ia rivers, with a great deal of sediment and nutrient input from the actively eroding Andes and Coastal Range are the most biologically productive of the Orinoco tributaries. Type Ib and II rivers drain the relatively nutrient poor regions of the high or aeolian plains llanos, or the Guayanan shield, respectively. The type Ia rivers invariably have a higher turbidity, electrical conductance, and ion concentration (e.g. nitrate, see appendix 4). Clearwater and especially blackwater rivers are well known for their chemical poorness and low biological productivity. Blackwater rivers are also quite acidic and contain high concentrations of plant secondary compounds, such as tannins which provide the characteristic dark water color. These rivers (e.g. Rio Negro, Rio Caroni) tend to have low levels of primary productivity and support depauperate faunas of invertebrates and vertebrates. Due to the limited availability of prey, blackwater rivers would be expected to be marginal habitat for large carnivores such as crocodilians. Indeed, few crocodilians are known from these habitats, with *Paleosuchus* being a notable exception.

Clearwater rivers may be only a less extreme example of blackwater habitats in terms of providing marginal crocodilian habitat.

Although chemically poor, and usually slightly acidic, clearwater rivers tend to have higher levels of primary productivity, and support larger invertebrate and vertebrate faunas (e.g. see Sioli 1968). Crocodiles are known from these clearwater rivers (types Ib and IIb), although in low densities. The factors resulting in reduced crocodile densities are probably several, but may include reduced food availability and possibly higher predation rates on young crocodiles from visually oriented aquatic and terrestrial predators.

Although principally found in the larger rivers, crocodiles were also known to enter smaller rivers and caños. During the dry season, these smaller water courses are frequently reduced to intermittent streams, or a series of interconnected pools ("charcos"). Under these conditions crocodiles would dig burrows and aestivate during much of the dry season (section 4.124). Crocodiles have been reported from both turbid water caños, as well as clear water caños, especially within the type Ib drainages.

Crocodiles were also reported by caimaneros to occupy oxbow lakes ("madre viejas") along the Orinoco and its major tributaries. Medem (1981) reports that during the wet season, crocodiles would move out of the rivers and into adjacent lakes, or remain in large river meanders where the current is less pronounced. Accounts of early naturalists suggest that during the floods of the wet season, crocodiles commonly dispersed away from the main rivers and caños that form the dry season habitat (Humboldt 1860, Paez 1868). With the drying of the savannas, most of the crocodiles were reported to return to permanent water sites, but some would apparently bury themselves in drying mud and aestivate in interior savanna habitats (Humboldt 1860). Presently, there appears to be little usage by crocodiles of these habitats during the dry season. Along the Rio Capanaparo, the only madre viejas found to contain crocodiles were those of very recent origin. These bodies of water still had many riverine characteristics (e.g. deep, open water and sandy beaches), but also supported dense *Caiman* populations. It is perhaps significant that only adult crocodiles were observed in these areas (section 4.121).

The use of lacustrine habitats far removed from river floodplains is not well known. Many lakes are found in the lower llanos region, but are usually connected with rivers during the rainy season. Several large lakes in the aeolian llanos between the Rio Cunaviche and the Cinaruco exist (Laguna Union Rodriguez, Laguna Rojero). Unconfirmed reports by campesinos and several airplane pilots suggest that a few crocodiles may have been found in these lakes at one time. Nevertheless, these areas can be considered unimportant habitat types from a population status viewpoint.

4.12 Microhabitat

Within the broad definition of macrohabitat as discussed above, crocodiles have definite preferences for certain environmental conditions that define their preferred microhabitat. A wide variety of biotic and abiotic factors may influence the distribution of crocodiles within the habitat. Some parameters are related to the physical environment: amount and distribution of vegetation, physical shoreline characteristics, water depth and gradient, degree of wave action, and the availability of basking and/or nesting sites are probably among the most important. Social factors such as territoriality may also be critical determinants of habitat usage patterns. Other biotic factors, including food availability and the degree of harassment by people, are often among the most important, but most difficult, parameters to quantify in the study of crocodilian habitat relations.

The results presented in this section are based primarily on data from nocturnal and aerial censuses of crocodiles in the Rio Capanaparo during the 1987 dry season. Hence, habitat selection is examined principally with respect to certain easily quantifiable habitat parameters. Comparative data from other areas is presented whenever possible.

4.121 Rio Capanaparo

The Rio Capanaparo during the dry season is a relatively shallow, meandering river with extensive sand beaches and bars. The river provides excellent crocodile habitat in several respects. Although it receives much of its drainage from type Ib tributaries, the Capanaparo also drains Andean piedmont regions in Colombia and so has some characteristics of type Ia rivers. The sand beaches and bars provide numerous nesting and basking sites for crocodiles. Good feeding areas are found where sand bars narrow the river and force it to move rapidly in shallow sections. Perhaps most importantly, the region is relatively remote and sparsely settled. The river is rarely used by people during the dry season as a route of transportation because it is too shallow for any but the smallest boats.

a. Position During Morning Basking. Aerial surveys of the river in April 1987 were used to collect ecological data on population size-structure, and habitat usage. Habitat data were obtained by marking the position of crocodiles on 1:100,000 maps and placing crocodiles in one of 5 situation categories: 1&2) On shore (OS sandbar, OS rivershore), 3&4) Shallow water on edge (SWOE sandbar, SWOE rivershore), and 5) In water (IW). A total of 101 situation sightings were recorded in the Capanaparo and its major tributary the Rio Riecito (Table 10). Forty crocodiles (39.6%) over 1.5 m TL were observed OS sandbars, and 37 (36.7%) OS rivershore. Considering that rivershore beach basking sites were much more abundant than sandbars, this suggests a preference for basking on bars. Assuming that virtually all basking crocodiles over 2.0 m TL were observed during the aerial surveys, the calculated sighting fraction of 27% (section 3.43), and the combined 76.3% total observed basking, indicate that some 20% of the crocodile population over 2.0 m TL are basking during the morning peak period (0830-1100 h). Because they were less visible than basking crocodile, smaller numbers of crocodiles were seen SWOE, or IW (Table 10).

b. Location Within the River. Crocodile locations within the river were separated into 4 categories: 1) river bends, 2) straight

river sections, 3) adjacent midstream islands, and 4) adjacent the mouths of caños or oxbow lakes. When crocodile position overlapped 2 or more categories, a subjective selection was made of the most characteristic category. A total of 95 sightings were divided among these categories (Table 11). Crocodiles appeared to prefer bends in the river (45.3% of the sightings), and the areas adjacent midstream islands (22.1%). Crocodiles appeared proportionally underrepresented along the straight river sections (24.2%). In river bends, crocodiles were almost invariably located along the lesser curvature of the bend, where extensive sand beaches and shallow water habitat were found. River bends provided protection from wind-generated wave action, which usually reached its maximum along the straight river sections, and also contained deep pools which would serve as refugia for crocodiles and their prey.

A total of 19 of the 21 sightings in the mid-stream island category (as opposed to sandbars) were adjacent to 3 islands in section 3, where the densest population was found. Here the river split into 2 channels of comparatively fast moving water, which may provide better fishing opportunities for the crocodiles. Crocodiles were usually associated with the downstream end of the islands, and particularly favored the use of small mid-channel sandbars located next to deep pools. Two of the islands (15 sightings) were also located near known nesting beaches and may represent concentrations of reproductive females.

c. Density Along the River. As noted in section 3.43, crocodile sightings along the Capanaparo were divided into 10 sections downstream from the entrance of the Rio Riecito. Crocodile density varied considerably among these river sections, with the maximum density found in section 3 (Caño Amarillo-San Luis)(Tables 4-6,8). Throughout Venezuela, variability in crocodile density levels is less related to environmental factors and habitat preference than it is with human disturbance and predation intensity. This may also be the overriding factor in determining crocodile distribution in the Capanaparo. No crocodiles were observed in the lowest river section adjacent to the Rio Orinoco, the most heavily settled part of the river. Also, the lower region of the Capanaparo is passable by boats throughout the year and hence is more frequently used as a means of transportation. Crocodiles were reported in this part of the river by campesinos, but apparently are very wary and difficult to see. In contrast, along the upper and middle sections of the rivers, crocodiles are disturbed less by the local people and have a greater tendency to haul out and bask. The highest crocodiles densities were found in these much more sparsely populated upriver sections (2-4).

d. Nocturnal Habitat Usage. During nocturnal spotlight counts in river section 3 in February 1987, data on habitat usage were collected for non-hatchling crocodiles and Caiman. The environmental parameters noted for each crocodilian are listed in Appendix 5, but basic habitat subdivisions were based on crocodile situation, shore conformation, and degree of wave exposure. Data were collected for the main river channel, as well as in 3 oxbow lakes (madre viejas) with connections to the river.

Crocodile situation was classified into 5 categories: 1) on shore-OS, 2) in water among dead trees-DT, 3) in herbaceous vegetation in the water-IVIW, 4) in shallow water along an open shoreline-SWOE, and 5) in open water-IW. This last category was further subdivided based on the distance from the nearest shoreline: <1 meter, 1-5 m, and >5 m.

Crocodiles were almost always observed in open water (32 of 34 sightings)(Table 12). In both the main river channel as well as the madre viejas, approximately two-thirds of the crocodiles were first observed more than 5 meters from the nearest shore. Only one crocodile was seen in shallow water along the shore, and one adjacent a dead tree that had fallen into the water. One potential bias here is that many larger crocodiles are very wary of approaching boats and would immediately seek deep water when approached. However, in virtually all cases where a distant eyeshine was seen to submerge, the animal was in open water.

In stark contrast, Caiman in the river were much more closely tied to the immediate shoreline (Table 12). Only 15% of the Caiman observed were classified as IW, and half of these were within 1 meter of the shore. In fact, during the nocturnal censuses (normally conducted between 2000-2200 h), 40% of the Caiman seen were on shore, completely out of the water. No crocodiles were ever seen out of the water at night. In the madre viejas, where crocodile density was less and Caiman densities much higher than in the river, a larger percentage of the Caiman were seen in open water (48%), and fewer on shore (7%).

Data on shore conformation were recorded for all crocodilians less than 5 meters from the shore. Conformation was divided into 3 parts: 1) shore gradient (steep, moderate, low), 2) the nature of the shore-water interface (see appendix 5), and 3) the soil type. In the river, crocodiles showed a strong preference for low gradient shorelines (Table 13), especially along open sandy beaches or bars (Tables 14,15). Principally due to the lack of these areas in madre viejas, crocodiles were seen more frequently along steep, or moderate shore gradients, and avoided the shallow water, muddy low gradient areas. Caiman had a much greater tendency to be found along steep, or moderate gradient shorelines, especially under overhanging trees in areas of organic, as opposed to sandy, soils (Tables 12-14). These same generalizations can be made for Caiman in the madre viejas.

The narrow, straight river sections lined by semi-aquatic shrubs (Coccoloba sp.) or trees (Campsiandra comosa) were avoided by crocodiles, but were frequented by Caiman. Crocodiles were more typically seen in the broad, open sandy river sections, particularly near river bends or adjacent mid-channel islands. These data are in agreement with the daytime observations made during aerial surveys.

Certain differences were noted in habitat selection between hatchling, juvenile and subadult/adult crocodiles. In April 1987, 3 groups of hatchlings were encountered in the Rio Capanaparo. All had hatched no more than one week prior to being found, and all were still located within 150 m of the nest site, and had an attendant adult nearby. Hatchlings were found exclusively on shore or in shallow water along sandy shores among shoreline shrubs (usually Coccoloba sp.).

Juvenile crocodiles, like hatchlings, were found exclusively in the river, but tended to prefer the open, sandy river sections where they usually could be seen in shallow water. No juvenile crocodiles (<1.5 m TL) were ever seen in madre viejas. As mentioned above, adult crocodiles preferred the open sandy river sections, but were frequently seen in mid-channel. Adult crocodiles would also enter recently formed madre viejas that still retained many riverine characteristics (e.g. sandy beaches, deep, non-muddy water). Crocodiles avoid the later successional stages of madre viejas, which turn gradually into shallow, muddy swamps. These areas form ideal Caiman habitat.

4.122 Other Rivers.

Data on crocodile habitat preference from other rivers is less detailed than that presented for the Capanaparo. However, some data are available from several areas.

a. Rio Tucupido. The Rio Tucupido is a small tributary of the Rio Guanare in Portuguesa state. Crocodiles are found in a small piedmont section of the river located upstream from the crossing of the national highway southwest of Guanare. The Tucupido here is a narrow, shallow rocky stream that runs through dense evergreen forest. During the dry season adult crocodiles are restricted to the deeper, slower moving charcos that are distributed at irregular intervals along the river. Juvenile crocodiles are seen in the charcos, or in adjacent shallow, fast moving water. Adults bask on extensive, sandy beaches associated with the charcos, and have also been reported to use dens or burrows during periods of low water (see section 4.124).

b. Rio Caura. The Caura is a large southern tributary of the Orinoco in Bolivar state. The Caura has some properties of a blackwater river (dark, tannin stained waters) but limnologically is more similar to clearwater systems (Appendix 4). According to local residents, crocodiles were at one time found in the downstream river section, but now only remain between the first set of rapids at Las Trincheras, and the large waterfall, Salto Para. Within this river section, the Caura is very rocky, and has many stretches of rapids or fast water. During aerial surveys in 1986, crocodiles were only seen in the calm water sections between rapids. Crocodiles appeared to avoid the long river stretches with dense, forested banks and few sandbars. In general agreement with the findings of Franz et al (1985), crocodiles were usually seen in one of three microhabitats: 1) in deep charcos adjacent to mid-stream islands, 2) associated with sandbars on the upstream point of mid-stream islands, or 3) along the river shore, again usually associated with sandbars that form in small bays or along river curves. Only one juvenile crocodile was seen during nocturnal surveys, a 1.0-1.5 m individual seen in the water adjacent a large sand beach at the foot of Salto Para.

C. Rio Guarico/Orituco. Small, scattered crocodile populations are still found in the Rio Guarico drainage. Crocodiles in the Caño

Rabanal, through which the present course of the Guarico drains, occupy deep, slow moving charcos. In this area as well as in the Orituco, which dries into a series of interconnected charcos, crocodiles are known to dig burrows into the river bank for use as diurnal refugia.

4.123 Reservoirs.

Orinoco crocodiles are found in at least one reservoir (Embalse de Camatagua, Aragua state), and are strongly suspected to be in others (Embalse de Guarico, Embalse de Bocono), and will occupy the Tucupido reservoir when it is finished.

Reservoirs in general provide sub-optimal crocodile habitat. The lacustrine environment, with abundant dead woody, and live herbaceous vegetation, steep shoreline gradients, and lack of sandy beaches all favor *Caiman* instead of crocodiles. Indeed, the Camatagua Embalse has a very high year-round *Caiman* density (12.6-16.1 non-hatchlings per km), and nocturnal spotlight counts reveal an almost total lack of juvenile crocodiles. Adult crocodiles, observed during aerial surveys were either seen in shallow water atop floating mats of *Chara* (78.9%), or in open, deep water (21.1%). The floating mats of vegetation apparently provide shallow water resting areas in lieu of shallow gradient shoreline. In many areas holes through the mats were visible adjacent to shallow depressions that served as resting spots for crocodiles. Access to the top of the mats may either be through the holes or by crawling atop the mats. During the day the water on top of the mats heats rapidly as the vegetation provides a barrier against convective heat exchange. These conditions allow crocodiles to warm rapidly in the morning, but may lead to temperature stress in the heat of the day. Nevertheless, crocodiles have been observed atop these mats during afternoon aerial surveys.

4.124 Use and Construction of Burrows.

Under conditions of potential water stress (e.g. low, stagnant water conditions), crocodiles will construct "dens", or burrows back into the riverbank. Medem (1981) reported that crocodiles would use natural cavities carved into riverbanks by the current. But active construction of dens is reported by Godshalk (1978), and has been observed during this study. Burrows are usually dug into riverbanks that have a sharp dropoff, or where the river current has undercut the bank. Excavation of riverbank soil is accomplished using the front feet and snout. Material is scraped away in this manner and sediments are removed from the burrow by using vigorous undulating motions of the body and tail. This movement creates a current that carries material backwards and away from the digging site. The maximum size of burrows is unknown, but under captive conditions some are at least 7-8 meters in length (Medem (1981) reports a *C. acutus* burrow with a large terminal chamber 8.5 x 7.2 meters in size). The entrance is typically located underwater, and the burrows normally angle up above the watertable to provide an airspace within. During conditions of low water, the den entrances may become visible from the surface.

In the wild, Orinoco crocodiles apparently only dig burrows when they live in small, intermittent streams or caños that are subject to seasonal drying. Burrows have been reported from small, clearwater caños in Apure such as the Rio Quitaparo and the Rio Claro, the Rio Orituco and Caño Rabanal in the Rio Guarico drainage, the Rio Tucupido, the Rio Cojedes (Godshalk 1978). In many of these areas, the water courses seasonally dry up into a series of pools with little or no current. Under captive conditions in earthen ponds, Orinoco crocodiles will frequently dig burrows. Crocodiles in the lower sections of the larger rivers such as the Orinoco, Apure, and Capanaparo are not reported to dig burrows. Medem (1981) reports that dens are unknown to residents from the Guayabero-Guaviare system.

Up to 3 adult crocodiles have been reported to use the same burrow (Medem 1981), at times with up to 15-20 turtles (*Podocnemis vogli*). In the Rio Tucupido in January 1985, a 3 meter male crocodile was killed by poachers in a burrow together with an adult female.

Although it is well documented that crocodiles dig burrows, the use of dens is not well understood. Crocodiles probably use them on a regular or intermittent basis during the dry season as diurnal retreat sites, leaving the burrows during the morning and/or afternoon to bask, and at night to forage. Under very low water conditions, or if the animal is under energy stress, crocodiles may enter a torpid state and aestivate in the dens. Caimaneros would take advantage of this fact and pull aestivating crocodiles out of burrows if they found them in a torpid state.

Crocodiles were also reported by early explorers to aestivate by burying themselves in drying mud (e.g. Humboldt 1860). This was noted by Humboldt to be especially common in regions of interior savannas away from the main river courses.

4.2 POPULATION ECOLOGY

4.21 Population Density

4.211 Rio Capanaparo

Most crocodile populations in Venezuela are extremely dispersed due to past hunting, and little or no subsequent population recovery. Only two riverine populations with relatively high densities were studied: the Rio Capanaparo and the Rio Tucupido. Non-hatchling crocodile density in the Rio Capanaparo was calculated on the basis of aerial surveys (utilizing a correction factor to estimate the fraction of unseen animals) for crocodiles over 1 m TL (Section 3.432). The proportion of smaller animals in the population was estimated from the size-class distribution of crocodiles seen during nocturnal censuses in river section 3. Calculated values of non-hatchling density for the 10 river sections are presented in Table 8. The highest crocodile density, 4.10 crocodiles/km, was encountered in river section 3. The lowest density was in the river section adjacent to the Rio Orinoco, where no crocodiles were observed (0.00/km). The mean calculated density for the 10 river sections was 0.81/km.

Uncorrected nocturnal census data for river section 3 reveal a non-hatchling density of 1.64/km. Using size-class specific sighting fraction estimates for nocturnal surveys that were derived for Saltwater crocodiles in Australia (Bayliss et al. 1986), the estimated non-hatchling population in river section 3 is 114 (4.56/km)(Table 9), in general agreement with the 102 crocodiles estimated from aerial surveys.

During April 1987, nocturnal censuses in river section 3 revealed the presence of 74 hatchling in two distinct pods associated with recently opened nests. Over a total of 25 km this represents a mean density of 2.96 hatchlings/km.

4.212 Rio Tucupido

Little or no hunting for crocodiles was done on the Tucupido prior to the early 1980's. Estimates of population density in the Rio Tucupido suggest that it still contains a relatively healthy crocodile population. Total uncorrected population density was estimated to be 1.95/km. This estimate was based on aerial surveys (adult/subadult density 0.61/km), and nocturnal counts (juvenile density 1.35/km). These values represent the highest uncorrected population density for Orinoco crocodiles obtained during this study.

Estimates of the sighting fraction derived for the Rio Capanaparo may not be applicable to this population because the differences in the physical habitat are substantial. Also, the Tucupido is a fairly cool water river and hence a greater proportion of the crocodile population may be out basking at any one time, resulting in a higher sighting fraction. Nevertheless, using conservative estimates of sighting fractions (0.4 for aerial survey. 0.7 nocturnal census), non-hatchling crocodile density in the Rio Tucupido is roughly 3.44/km.

4.213 Other Rivers

Uncorrected population density values for rivers surveyed by fixed wing aircraft are presented in table 2. Most of these other rivers have extremely low population densities, that would be considerably below 0.1/km even if correction formulae were applied. Nocturnal surveys disclosed crocodiles in several other areas, again at very low densities (Camatagua reservoir 0.05/km, Rio Caura 0.167). One locally dense crocodile "population" was found in the Rio Orituco, with 4 crocodiles seen in two adjacent river charcos (2.3 km, density= 1.74/km).

4.22 Population Size Structure

Crocodiles sighted during the census work were assigned to size-class categories. Because nocturnal census work permitted a better estimation of crocodile size, these categories were broken into 0.5 m intervals. During aerial censuses, 1 meter size-classes were used to reduce potential error. Table 16 summarizes size-class distribution data from nocturnal surveys (2 populations), and aerial surveys (4 populations).

The most complete information on population structure is from the Rio Capanaparo. Aerial surveys in 1986 revealed a larger number of 1-2 m crocodiles than did the more extensive 1987 surveys. Because the 1987 surveys had a much larger sample size (98 vs 38), it is assumed to be a better estimation of the true size-class distribution. Nevertheless, the combined nocturnal census data for 1987 perhaps reflect the best approximation of the size-class distribution. These data suggest that the population is composed of 38.5% juveniles (<1.5 m TL), 26.3% subadults (1.5-2.5 m TL), and 35.0% adults (>2.5 m TL, note: the subadult value is conservative, and the adult figure a slight overestimation as most males probably do not reach sexual maturity until they are 3 m TL).

During the April surveys, a total of 74 hatchlings were counted in river section 3. If we assume that 50-100 hatchlings were produced in the previous two years, and the 0.5-1.0 m size class represents two age-classes (see section 4.3) we can roughly estimate mortality as 91-95% over the first two years of life.

Based on the total population estimates, the size-class distribution of crocodiles in river section 3, and a calculated length-weight relationship from 37 captive crocodiles (SVL 17-193 cm), the population biomass of crocodiles in the Rio Capanaparo was calculated (Table 19). A length-weight relationship [Log_{10} mass = 3.16(Log_{10} SVL)-1.94 (r^2=0.995)], derived from captive Orinoco crocodiles (0.25-3.70 m TL) was used to estimate the biomass for the midpoint of each crocodile size-class, and then multiplied by the number of crocodiles in each size class for each river section. Biomass was determined for both river section 3, and the entire river below the Rio Riecito (sections 1-10). River section 3, which has by far the densest crocodile population had a total estimated biomass of 4,945.4 kg, or 197.8 kg per kilometer of river. The corresponding figures for the entire river were 11,301.8 kg, and 39.2 kg/km. The only other published values for crocodile biomass in a riverine habitat are for Crocodylus niloticus in the Victoria Nile (Parker and Watson 1970, 397.5 kg/km), and are considerably higher than the figures for C. intermedius in the Capanaparo.

Survey data from the Rio Tucupido reveal a much more truncated size-class distribution. The largest individuals seen during aerial censuses were in the 2-3 m size class, and the majority of crocodiles observed were in the 1-2 m juvenile-subadult category. Nocturnal counts also showed a large percentage of juveniles (84.6%), and only 15.4% of the crocodiles seen were over 2 m TL. The low number of adult crocodiles observed during the nocturnal counts may reflect their extreme wariness due to recent hunting. However, based on the aerial surveys it appears that the Tucupido has very few large crocodiles (>3 m TL). This may suggest one of several things: 1) the Tucupido crocodiles do not attain large sizes and represent an isolated deme of small-sized crocodiles adapted for living in a piedmont river, 2) most of the large crocodiles have been recently killed or have emigrated to other areas, or 3) the large crocodiles are extremely wary and rarely seen. These hypotheses are not mutually exclusive, and more than one factor may be applicable to this situation. However, with respect to hypothesis 1, it is known that some crocodiles in the Tucupido are at least 3 m TL. One 3 m TL specimen was killed in a burrow by poachers in January 1985. Nevertheless, some evidence exists indicating that growth rates among hatchling and yearling crocodiles in the Tucupido is fairly low (see Section 4.232), and crocodiles here may not attain very large sizes.

The size-class distribution of crocodiles in the Camatagua Embalse is intermediate with respect to the Tucupido and the Capanaparo populations. The relatively large number of 1-2 m crocodiles seen in the reservoir from the airplane (31.6% of the sightings), contrasts sharply with the complete absence of juveniles during nocturnal counts. The aerial survey results appear to indicate that despite the poor physical habitat, the lack of good nesting beaches, and the presence of many potential predators of crocodile hatchlings (Caiman, piraña), that some recruitment into the adult population is taking place. However, this is not borne out by the results of the nocturnal surveys, and more work needs to be done in the Camatagua reservoir to determine the state of the crocodile population.

4.23 Growth Rates

4.231 Captive Crocodiles.

Virtually all the available data on growth rates of Orinoco crocodiles comes from captive animals. On Hato Masaguaral, all juvenile crocodiles are periodically measured and weighed to calculate growth rates. Adult crocodiles are also remeasured periodically. Also, data have been collected on ecological growth efficiency, measuring the amount of food ingested, and the resulting change in weight of the animals (food conversion efficiency). Both growth rates and growth efficiency are based on crocodiles fed a diet of ground fish mixed with a vitamin supplement.

Average growth rates of captive hatchling crocodiles ranges from a high of 0.060 cm snout-vent length (SVL)/day, to a low of 0.023 cm SVL/day. The maximum values correspond to an annual total length growth rate of 40-45 cm. Individual crocodiles have demonstrated growth rates of up to 0.075 cm SVL/day, which would result in a annual total length growth rate of 55 cm. Yearling crocodiles have shown similar mean growth rates of 0.013-0.060 cm SVL/day, again with certain animals growing up to 0.075 cm SVL/day. Over this same period ecological growth efficiency was calculated to be 12.0% [(mass of food ingested/change in crocodile biomass) x 100)].

One hatchling that escaped from the breeding enclosure shortly after the female opened the nest, lived in the wild for a period of 218 days before being captured on 15 Dec. 1985. This individual grew at a rate of 0.076 cm SVL/day, and at the end of one year was 72 cm long (TL). This indicates that in the wild under favorable conditions, hatchling Orinoco crocodiles can grow at a very rapid pace. High growth rates can apparently be maintained at least through the first 3 years of life. Ayarzaguena (1984) reports an Orinoco crocodile in Hato El Frio that after 3 years measured 1.48 m TL, for a growth rate of 0.104 cm TL/day over the three year period.

Under captive conditions, non-juvenile crocodiles can still maintain relatively high growth rates. The average growth rate among 5 female Orinoco crocodiles ranging from 95.3-120.5 cm SVL (all 7 years old) was 0.040 cm SVL/day over a 450 day period on Hato Masaguaral. Assuming that when born, the crocodiles measured 15 cm SVL and 30 cm TL, we can calculate the mean growth rate of these and 6 other female crocodiles to their 7th year (Table 17). The resulting mean growth rate is 0.036 cm SVL/day, or 0.064 cm TL/day for those with complete tails. This translates into an average annual increment of 23 cm TL, despite the fact that for several years they had been kept under very crowded conditions. Similar data for a captive reared male housed on Hato Masaguaral (Table 18) indicates a comparable growth rate over its first 6 years of life, (0.065 cm TL/day) after which growth slows somewhat. However, to an age of 15 years, 10 months this individual maintained an average growth rate of 0.049 cm TL/day (total length 3.14 m).

Based on data from captive animals, sexual maturity is attained in females at a length of approximately 2.4-2.6 m TL, and 3.0 m TL for males. Assuming the growth rates for these captive specimens are similar to wild individuals, maturity could be attained in as little as 7-10 years in females, and 9-12 years for males.

4.232 Wild Crocodiles

Little data exists on growth rates of free-ranging crocodiles. As no recapture data of wild crocodiles are available from this or other studies, values have to be derived by estimating the ages of captured juvenile crocodiles. These estimates were made for 4 juvenile crocodiles in the Rio Capanaparo and a similar number in the Rio Tucupido.

Captured small juvenile crocodiles in the Rio Capanaparo could be split into 2 size-classes with snout-vent lengths of 35-43 cm, and 50-60 cm. As no crocodiles were seen intermediate in size between these and hatchlings (15 cm SVL), it was presumed that these represented 1 and 2 year old crocodiles respectively. Based upon this assumption, the mean growth rates were calculated to be 0.076 cm

SVL/day for the yearlings, and 0.057 cm SVL/day for the 2 year olds. These values compare well with the higher growth rates of captive crocodiles, and appear very reasonable in view of the rapid growth found in the two free-living crocodiles reported in the previous section.

In the Rio Tucupido (April 1986), it appeared that juveniles could also be split into two size-classes: 25-30 cm SVL, and 45-50 cm SVL. The smaller size-class was assumed to represent one year old animals, and the mean calculated growth for these individuals was 0.031 cm SVL/day. However, the larger size-class is more difficult to classify. If we assume they are two years old, then we find a significant increase in growth rate during the second year of life (0.042 and 0.046 cm SVL/day). If they are calculated to be three years old, we find growth similar to the yearlings (0.029 and 0.031). As reproduction in the Tucupido is dependent on a relatively small number of females, it is not unreasonable to assume that one year class of juveniles was missing from the section of the river surveyed (7.0 km), and that the slower of the two calculated growth rates applies. In either case, the growth of juvenile crocodiles in the Rio Tucupido appears to be slower than in the Rio Capanaparo.

If these are real differences, and are maintained throughout the life of the crocodiles, it may partially explain the lack of large crocodiles noted in this river during aerial and nocturnal censuses.

4.3 REPRODUCTIVE ECOLOGY

4.31 Courtship and Mating.

Observations on courtship and mating of a captive pair of Orinoco crocodiles (male 3.65 m TL, female 3.02 m TL) have been made on Hato Masaguaral over the period November 1984 to July 1987. Some additional observations were made on a second adult male (3.0 m TL) housed with a group of adult and subadult females. This section will discuss two principal topics, the male advertisement display (jaw slaps/roars), and courtship and mating behaviors.

4.311 Male Advertisement Display.

The principal advertisement display (AD) of male Orinoco crocodiles consists of a combination of jaw slaps, and loud roars. The sequence of behaviors involved in the display is typically as follows. The male slowly swims in open water in a "high float" posture, with the body inflated, head held high in the water, the dorsal surface of the body and tail out of the water. The tail is slowly sculled back and forth in an exaggerated fashion as the male patrols in this posture. At times, the male may produce short bursts of sub-audible vibrations (SAV) which cause the water on the surface of his back to vibrate upwards in what is termed a "water dance" (Vliet 1986). These SAV's are of very low frequency (probably 10-15 Hz) and are below the range of human hearing, rather they are felt by transmission through the water and ground. Figure 3 presents a sonogram of a male advertisement display with 2 jawslaps followed by 5 roars.

When ready to give the AD, the male will approach the shore and stop in shallow water, oriented perpendicular to the shore, usually with his head 0.5-1.0 m from the shoreline. He may remain in this position for several minutes before slowly raising the tail, then the head, holding the rear (angular) region of the head higher, and opening the mouth slightly. Before jaw slapping, the head, and the distal two-thirds of the tail are raised almost entirely out of the water. From this stereotypic head-elevated tail elevated posture (HETE), the male will usually "tail wag" briefly, then forcefully slap its upper jaw down against the surface of the water, at the same time rapidly closing its mouth to increase the force of the impact. This "jaw slap" produces a loud, distinctive noise, and is usually performed twice in rapid succession (mean=1.93, range=1-3, n=312 observations). Immediately following the jaw slaps the male will raise the tip of its snout, angling its head upwards with the mouth agape and roar 3-4 times (mean=3.39, range=1-6, n=314 observations). Roars have a deep, throaty, sonorous quality, and are given with a slowing cadence and declining volume. Most of the sound energy of the roars is concentrated between 50 and 250 Hz (Figure 3).

Associated with each roar, the male drops its body slightly in the water and tilts its head upwards. Between roars the male will raise its body and drop its head slightly. A full sequence of 2 jawslaps and 3-4 roars usually lasts 8-10 seconds. Following the roars the male drops its head and tail to water level, and frequently blows bubbles out through its jaws. Occasionally this is accompanied by a forceful sculling of its tail in the water.

Infrequently, the male would produce roars while on land. These were not part of an advertisement display, but were made in response to loud, low frequency noises (e.g. explosions).

Females were never observed to make advertisement displays, and the only observations of females assuming the high float posture were in association with nest protection. Females apparently do have the capability to roar and have been heard to do so on occasion in response to loud noises.

Because the AD produced a loud noise, and the crocodile breeding enclosures on Hato Masaguaral were located immediately adjacent to the house, AD could be heard throughout the day (waking up the researchers at night) and as a result 24 hour observations on AD frequency were made.

The AD is principally given at night, especially early in the morning shortly before dawn (Figure 4). An analysis of 484 AD from two males on Hato Masaguaral reveals that only 71 (14.7%) AD were recorded during daylight hours (0700-1800 h). AD frequency increases after 1900 h, reaching a small peak from 2100-2200 h, then declined slightly 2200-0100. After 0100 h AD frequency would again increase, and reached an overall peak around dawn (0600-0700, 119 AD, 24.6%).

On an annual basis, AD are given throughout the year, but reach a peak during the courtship and mating period (September-February, Figure 5). The frequency of 327 observed AD on Hato Masaguaral during 1985-1986 reveals that 82.6% of the AD occur during these 5 months, with the peak month being January (24.5%).

The functions of advertisement displays are probably twofold (Garrick and Lang 1977). Firstly, they serve in the establishment of territories among males. Male territoriality among crocodilians appears to be mostly a seasonal behavior associated with reproduction. The AD serves as a system for communicating with other males information regarding territoriality. The successful establishment and defense of territories among male crocodiles is almost certainly related to size, with the larger crocodiles being dominant. The AD presumably can transmit information regarding the size of the crocodile based on the frequency and energy of sound produced.

Medem (1981) reports that male Orinoco crocodiles would establish territories, centered on deep river pools, and patrol these areas throughout the dry season. These pools would sometimes also contain a smaller individual, possibly representing a reproductive pair. Two large individuals (presumably males) were reported to patrol 2 and 0.5 km of river each (Caño Negro, upper Rio Capanaparo drainage in Colombia). Another large male (ca. 5 m TL) from the Rio Ariari was reported to have a territory of approximately 300 m (Medem 1958).

The AD may also be used to attract females for courtship. On Hato Masaguaral, if the female was in the water when a AD was given, she would frequently swim directly at the male and initiate courtship. Studies of other crocodilians in captivity and in the wild (see Garrick and Lang 1977 for review) indicate that females are not territorial, but enter and leave male territories, and under higher density situations will form breeding harems. However, in high density situations captive female Orinoco crocodiles will form

dominance hierarchies based on size and aggressiveness. The same information in the quality of sound produced by the AD may be used by females in choosing between potential mates.

The use of musk, produced by submaxillary and cloacal glands, in territoriality and courtship is not well understood. Musk is composed primarily of long chain fatty acids and may have at least two components, one that forms a thin film on the surface of the water, and another airborne fraction.

4.312 Courtship and Mating.

Crocodile courtship consists principally of a series of stereotyped behaviors that do not follow any particularly fixed sequence. In the breeding pair maintained at Hato Masaguaral, courtship was frequently initiated by the female following the male AD, or by the male actively approaching the female and producing sub-audible vibrations from a high float or head/tail elevated posture. However, other environmental stimuli such as the introduction of food, or pumping water into the pen would also start courtship. Unreceptive females would not respond the the male's approach, remaining immobile on the surface or would submerge. If the female was receptive, courtship activity would began with the pair slowly swimming in circles or engaging in snout rubbing. Upon initial contact both male and female would frequently emit snorting sounds which may serve as recognition signals, or the female would slightly angle her snout upwards. When snout rubbing, the female would rub the tip of her snout along the lateral surface of the male's snout. This was sometimes followed by the female riding her head atop the cranial table, the nuchal region or the snout of the male, occasionally pressing him underwater. The female would also rub the ventral surface of her head along the dorsal surface of the male's neck, back or pelvis region.

Continued courtship involved much circling behavior, snorts, snout-rubbing, bubbling, and repeated submerging and re-emergence. When re-emerging, the male would occasionally forcefully expel air from his lungs underwater, creating a loud bubbling noise, and continue as his head reached the surface, producing a hissing noise. More violent courtship-like activity, usually associated with the introduction of food, would involve energetic swimming, and mock biting. Under these conditions the female would frequently assume a submissive snout-lift posture, with the head held out of the water at a 45 degree angle.

While submerged, or less frequently while at the surface, the male would ride atop the female and assume a copulatory posture. The pair would then rise to the surface where copulation would occur. Early in the courtship season these pairings usually did not result in copulation, which was characterized by the male arching his body around the female's to oppose cloacas. From this posture the tip of the male's tail would protrude out of the water on the opposite side of the female. While copulating, the female would remain below the male, usually with the snout angled upwards and off to one side, alternately below or above the water's surface. While below the surface she would occasionally expel air through her mouth and bubble.

Copulation was frequently preceded by very little courtship activity. Copulations were seen most frequently during mid-December. The dates of 9 copulations seen on Hato Masaguaral are: 10, 18 December 1984, 3, 11, 17 December 1985 and 17 January 1986, and 24 November, 5 December 1986, and 2 January 1987.

4.32 Nesting Biology

4.321 General Nest Site Characteristics

Orinoco crocodiles typically nest in holes dug into sand beaches along riverbanks, or in river islands or sandbars. However, like other New World crocodiles, Orinoco crocodiles are quite adaptable with respect to the type of soil they can nest in. One unconfirmed report even exists of *C. intermedius* constructing a mound nest (Medem 1981). The following discussion will concentrate on the nesting ecology of Orinoco crocodiles in a fairly typical situation (the Rio Capanaparo). Following this there will be a brief examination of some atypical nesting situations.

a. Rio Capanaparo

The nesting biology of Orinoco crocodiles was studied during the dry season of 1987 in the section of the river between Caño Amarillo and Hato Las Mercedes (river section 3 and part of section 4), along a total of 37 km of river. In this area 6 definite nests, and 5 probable nests were located. Probable nests were divided into two groups: nests predated by humans before our arrival, and nests that did not hatch before our last visit to the area (30 April). Human predated nests were identified by the presence of human tracks, a deep excavated pit, and usually a nearby probe stick that was used to locate the eggs. Unhatched nests in late April were being regularly visited by female crocodiles. These nests were categorized by the presence of adult crocodile tracks ascending to a potential nesting area >3 m from the river. Basking crocodiles would rarely move more than 2 meters from the shore, and would usually bask on low sandbars where nesting does not occur.

The total estimated nest density over 37 km of the best crocodile habitat in the Capanaparo was 0.30/km. Along this same stretch of river 51.3% of the crocodile population in the Capanaparo was sighted. A rough estimate of the total number of crocodile nests over the 288 km of the Capanaparo that was surveyed in 1987 is 21 (0.07/km).

Crocodile nests were located in two distinctive situations: along the tops of undercut river banks (barrancas), or in elevated sandy beaches (playas) along the river shore. Crocodiles do not nest in low sand beaches nor on mid-channel bars. Six of the 11 nests (54.5%) found were located atop barrancas, 5 (45.5%) in elevated playas. Table 20 summarizes data collected from the 6 nests that were examined prior to hatching, or found hatched. One of the nests (#1) was predated by Indians before clutch data could be collected. Two other nests (#5, #6) were located after hatching and similarly lack clutch data.

Barranca nests were situated in deep sand atop steep banks where the river actively erodes into the surrounding mixed savanna/gallery forest habitat. These nests were always located along the greater curvature of river bends, and required a short steep climb by the female to reach the nest site. Mean height above the river level in April was 3.81 m (n= 3 nests), and straight-line distance to the rivershore averaged 8.6 m. The placement of nests well above the river level presumably serves to reduce potential flooding mortality. The nest cavities were located atop the barranca, close to the lip in 2 cases, and one nest (#4) was found in a small hollow just below the top of the barranca. The nest was usually found in the open, among sparse vegetation typical of open, sandy areas in the gallery forest (*Byrsonima crassifolia*, *Psidium crenatum*, *Couepia ovatifolia*), or shoreline vegetation (*Coccoloba* sp., *Campsiandra comosa*). The mean distance to the nearest tree (>2.5 m tall) was 3.0 m.

Because the Capanaparo has an abundance of potential nesting beaches, the distribution of nesting sites may reflect the juxtaposing of suitable nesting areas with preferred adult habitat. Two barranca nesting sites, only 2 km apart, had two nests each and were located near concentrations of adult crocodiles. According to Indians who regularly search for crocodile nests, the same nesting beaches are used year after year.

Nests on elevated playas were similarly situated well above the river (mean 3.07 m), although not as high as the barranca nests. These playas were high, well drained, deep sand areas located along the river banks (4 of 5 nests), or at the upstream point of an island closely associated with the rivershore (nest # 6). Mean distance to the rivershore in three playa nests was 10.5 m, and like the barranca nests they were situated in the open among sparse vegetation (mean distance to nearest tree=3.0 m).

Nests holes varied between 64-45 cm deep, with the top of the egg clutch 25-45 cm below the surface of the sand (Table 20). Of three clutches found intact, two were quite large (65, 58 eggs), and one very small (21 eggs), for an overall mean of 48.0 eggs. Based on egg banding, fertility in the three clutches ranged from 95.2 to 100.0% (mean=97.4%).

The crocodile eggs were quite large (mean mass=119.2g), and clutch mass ranged from 2386 g in the small clutch to 8017 g in the largest. A captive female crocodile on Hato Masaguaral laid clutches of 4.5%, and 4.6% of her body mass in 1986 and 1987. These data would indicate that the three nesting Capanaparo females weighed approximately 178, 155, and 53 kg each. Using the length-weight relationship derived for Hato Masaguaral crocodiles the snout-vent lengths of these females are estimated to be 1.89, 1.80, and 1.30 m.

Hatchlings were weighed from nests 2 and 4 within 2 days of hatching. Nest 3 hatchlings were probably weighed within 3-4 days of hatching. A comparison of egg weight with hatchling weight from these three nests reveals that hatchlings weigh 66-71% of the total mass of the eggs (eggs weighed 2-4 weeks after laying).

The peak period of egg laying in the Rio Capanaparo during 1987 was during the first week of February. Only one nest was found during a visit to the site on 28 January (eggs freshly laid, still with mucous), and the nests found in late February had been in the ground some 2-4 weeks (based on egg band width).

Most nests hatch the last week of April, or the first week of May. Hence, egg incubation lasts some 80-90 days. The 1985 Hato Masaguaral nest had a similar natural incubation period of 86 days. The 1987 Hato Masaguaral nest was incubated 78 days but the eggs were probably opened several days prematurely.

b. Other Areas.

Typical Sand Beach Nests. One crocodile nest was also found in the Rio Tucupido. This nest was located in a typical sand beach, and had already hatched when it was discovered on 28 April 1986. The nest was situated some 15 m from a deep river pool in which >14 hatchlings, two yearlings, one juvenile and an adult crocodile were all seen. The nest was not situated in a very elevated beach (<1.5 m above water level), and was located at the base of a small clump of grass (*Gynerium sagittatum*) in an otherwise exposed location more than 5 meters from the nearest tree.

Crocodiles in the Rio Orinoco were reported to nest in sandbars along the rivers' edge, island beaches, as well as in some of the larger mid-channel sandbars. Blohm (1982) reports finding a nest in the process of hatching on 19 April 1946, in a mid-channel sandbar near Isla Pararuma. The nest was at the time being eroded away by the rising river waters.

Crocodiles were reported by Godshalk (1978) to nest in sandy beaches in the Rio Cojedes. One nest was found on 26 February 1978, and had 34 eggs in a nest hole 40 cm deep. Ayarzaguena (pers. comm.), has found crocodile nests in the Cojedes-Sarare system in beaches of sand mixed with organic material.

In the Rio Caura, Franz et al. (1985) found evidence of 3 freshly opened crocodile nests on 26 March 1982. All three nests were all located on an elevated sand bar. This bar was the largest, most elevated nesting beach in the stretch between Maripa and the Salto Para, and is also a favored nesting site for the large Orinoco river turtles (*Podocnemis expansa*). Nests were also reported by resident indians in other sand bars further upstream (pers. obs.). The opened nests and interviews with indians suggests that hatching occurs from late March to early April.

Medem (1981) reported finding a crocodile nest in an elevated sand beach on the lower Rio Guaviare. This nest contained 57 eggs, in a cavity 27-43 cm deep.

Atypical Nesting Habitat

During this study, one crocodile nest was located in the Camatagua Embalse, in a steep soil/talus slope along the edge of the reservoir. The soil was a clay-rock matrix that appeared to form an extremely poor nesting medium. However, the nest had succesfully hatched and a group of >25 hatchlings and an adult crocodile were observed along the shore immediately adjacent the nest. The nest cavity was 1.6 m above the reservoir level, and 3.3 m from the shore. In July 1980, Sr. Tomas Blohm found 3 opened nests in schist/clay soil along a recent road cut in a different section of the same reservoir. The three nests were found within 56 m of one another and all had apparently hatched successfully (Blohm 1982).

The flooding of the Camatagua reservoir in 1969 covered all the sand beaches formerly associated with the Rio Guarico, and left no typical nesting areas for the crocodiles. However, due to a large degree of flexibility in nesting requirements, the crocodiles have been able to successfully nest in marginal areas. This nesting flexibility may have been important in natural habitats which lack sandy beaches. Crocodiles in the Caño Rabanal (Rio Guarico) are reported by local residents to nest in organic soils along the river. The same has been mentioned for crocodiles in the Rio Pao, Cojedes state. Other rivers such as the Arauca and the Guariquito, once renown for their crocodile populations, do not have extensive sand beaches, so crocodiles may have been forced to nest in marginal areas.

Medem (1981) even mentions a report of an Orinoco crocodile building a mound nest from vegetation along the upper Rio Ariporo (Colombia) where no sandy beaches are found. The nest was a mound formed from dead branches and leaves, and had an attending adult (presumably female). However, this report, if true, repesents an unusual phenomenon that plays a minor role in overall nesting ecology. Rare vegetation mound nesting has also been reported for *C. acutus* (Alvarez del Toro 1974, Medem 1981).

4.322 Timing of Nesting

Orinoco crocodiles oviposit during the early dry season, (January-February), when river levels are dropping, exposing the preferred nesting areas. After an incubation period of 80-90 days, the nests are opened by the female prior to the flooding associated with the beginning of the wet season. Nesting during a period of falling water levels minimizes the risk of nest flooding. This nesting schedule also insures that the young hatch near the start of the wet season, during a time of increased habitat and food availability. For instance in the Rio Capanaparo, hatchling crocodiles have been observed feeding on insect hatches (Ephemeroptera) following rains.

Within this general pattern, Orinoco crocodiles appear to show a moderate degree of variability in the timing of nests. Throughout the range of Orinoco crocodile, egg laying is reported over a 2 month period. Some data suggests that nest timing may be related to the annual flooding regime of the rivers involved. This analysis must be considered preliminary as only scanty information exists on the actual timing of crocodile nests in many parts of the species' range. Nevertheless, with data from this study, and a review of published information, an initial analysis can be made.

Crocodile nesting can be roughly divided into three temporal categories based on the date of hatching (for which more data are available): early nesters (hatch mid-late March), late nesters (hatch late April-early May), and median nesters (hatch early-mid April). Early nesters have been reported from most of the Colombian Orinoco basin (Medem 1958), and the Rio Caura (Franz et al. 1985). The Rio Tucupido population is apparently early-median (nests at the UNELLEZ Guanare captive breeding center hatch the last week of March-first week of April). The Rio Orinoco crocodiles were evidently median nesters (Humboldt 1860, Blohm 1948). Late nesters have been reported from the Rio Capanaparo (this study), and the Rio Cojedes (Godshalk 1978, Ayarzaguena, pers. comm.).

Paralleling these differences in nesting schedules are corresponding contrasts in the hydrological regimes of the rivers involved. Utilizing data from the Direccion de Hidrologia (MARNR), the Rio Orinoco and its major tributaries can be divided into 3 basic types depending on when they show the first increases in water level associated with the rainy season. The data analyses examine maximum monthly water levels over a 7 year period (1978-1984). Maximum water levels were used as they more accurately reflect the threat of nest flooding.

"Early" rivers begin to rise in March (e.g. Rio Meta, Rio Arauca). "Late" rivers may rise slightly in April, but do not show significant increases until May (e.g. Rio Capanaparo, Rio Cojedes). The Orinoco and some of its major tributaries (e,g, Rio Apure) are intermediate and demonstrate dropping level in March, but showing significant increases in April (Table 21).

Rivers with a significant portion of their drainage coming from Andean regions (especially the Colombian Andes) tend to be early rivers. Internal llanos drainages tend to be late rivers, as do rivers draining the northern Coastal range. Rivers such as the Orinoco and Apure which drain diverse areas tend to be intermediate in character. Although the data are very incomplete, in Venezuela, crocodiles in early rivers appear to nest early, and nest late in late rivers (Table 22). Among the rivers reported for Venezuela, the only possible exception to this general relationship is the Rio Caura, where crocodiles hatch relatively early. The water level data seem to indicate that the Caura has an intermediate flooding regime, dropping in March, but rising significantly in April (Table 21). However, the data for individual years shows that on 3 of the 7 years, maximum March water levels increased over those of February, in one case 1.55 m. Also, the high relative standard deviation for February and March indicates maximum water levels during the dry season are very variable from year to year. These data indicate that the Caura is a somewhat less predictable river and may rise significantly prior to April, and to reduce flooding mortality crocodiles may nest early.

Additionally, Medem (1981) reports hatching dates of Orinoco crocodiles in Colombia as being early March to mid April. If we use the Rio Meta as being characteristic of the Colombian Andean rivers, we see that they tend to rise early, and hence the crocodiles nest early.

An important modifying factor for this analysis, and one for which few data are available, is the availability of elevated nesting sites. If high, well drained nesting beaches are available, crocodiles may tend to nest later, reducing flooding probability by placing the eggs well above the water level. Conversely, if only low, easily flooded sandbars are available for nesting, crocodiles may be forced to oviposit earlier.

This timing of nesting in relation to river level fluctuations suggests two points: 1) flooding can be an important source of nest mortality and has had an important effect on determining crocodile nesting schedules, and 2) crocodiles nest as late as possible. The latter point is suggested by the fact that crocodiles from "late"

rivers do not nest over a greater period of time. In some populations crocodiles hatch in mid-late March, indicating that oviposition in these cases takes place near the end of December. Crocodiles in late rivers could potentially nest earlier, but the minimal reduction in flooding probability may be more than offset by the risk of exposing newly hatched young to a longer period of late dry seson low water conditions. Thus the nesting schedule appears to be shaped principally by two factors, flooding mortality of eggs and hatchling survivorship over the first critical months. In this respect, nesting schedules appear to be designed to reduce the overall mortality resulting from nest flooding and early hatchling death.

4.323 Nesting Behavior and Parental Care

a. Nest Excavation

Female crocodiles begin visiting potential nest sites several weeks before nesting. During these nocturnal visits the females will walk around potential nesting areas and make trial excavations. In captivity, and presumably in the wild, nesting is usually preceded by several nights of increased activity, during which time the female makes more extensive excavations and spends many hours atop the nest site.

Observations of nesting behavior were made at Hato Masaguaral in 1985 and 1986. On 20 February 1986 at 0845 h the female was observed atop the nest mound in the process of egg-laying. She was positioned with her ventral surface pressed close to the ground, head cocked up in an "alert" posture with the mouth slightly opened, and her hind legs folded back along the ventro-lateral surface of her tail. Slow, irregular contractions of the abdomen were visible, mixed with occasional deeper contractions and a slight uplifting of the pelvic/cloacal region. This latter movement was assumed to represent the passing of an egg through the pelvic canal, and during the observations the interval between these deep contractions increased from 30 seconds, to 1 min. 15 sec.

At 0913 h the female began making alternating digging motions in the air with her hind legs. At 0930 h she began pushing soil into the nest hole using a similar digging movements of the hind legs. Once the hole was almost filled, the female raised her pelvic region, and holding both hind legs almost directly under her, compacted the nest soil using a slow, walking motion, followed by scraping more soil onto the nest. This activity was repeated twice during the next 11 minutes. At 0950 h, the female began slowly walking forwards, alternately using her hind legs to scrape more soil atop the nest. At 0958 h, she circled around and laid down atop the nest cavity. During the next 15 minutes the female continued to lie atop the nest or periodically walk around the nest, scraping material with her hind legs. At 1017 h she left the nest site and entered the water. The female was later observed to re-emerge and scrape more material over the nest at 1055 h.

The same female oviposited during the morning hours on 24 February 1987, but oviposition in 1985 occurred at night. In the wild, crocodiles appear to nest invariably at night.

b. Defense of Nest Site

Little is known concerning nest defense in wild crocodiles. Few nest predators other than man have been reported in the literature, and no accounts exist of nest defense against non-human predators. Medem (1958) reports black vultures (*Coragyps atratus*) and tegu lizards (*Tupinambis teguixin*) as nest predators, however the former species seem unlikely. Other potential nest predators include foxes (*Cerdocyon thous*), and racoons (*Procyon cancrivora*).

In the wild, active defense of nests against humans is virtually unknown today. Indigenous peoples along the Rio Capanaparo regularly collect eggs from nests and do so without fear of attack by adults. However, in historic times crocodiles were known to be protective of the nest (Gumilla 1741, Verstraeten 1939), and in these situations would pose a significant danger to man.

In captivity, adult crocodiles will vigorously defend the nest site against human intruders (Blohm 1982, pers. obs.). Observations on Hato Masaguaral indicate it is the female that most frequently and actively defends the nest site. If the nest were approached, the female would almost invariably rush out of the water in a threatening fashion, and would frequently attempt to bite visitors through the fence. Under the same circumstances the male crocodile in the enclosure would occasionally assume a threat posture from in the water, but was never observed to charge out of the water.

c. Nest Opening Behavior

Observations of nest opening behavior were made in captivity on Hato Masaguaral on 11-12 May 1985. The female crocodile had been making nocturnal visits to the nest site for several days prior to opening the nest. On the night of 11 May, she emerged from the water prior to 2200 h, and was observed excavating the nest at 2232 h. As the nest was located immediately adjacent to the enclosure fence and the female was remarkably tolerant of human presence, observations were made from within 3 meters of the nest site without visibly disturbing her. The female used her front feet to scrape material out of the nest cavity, this material was then further removed from the nest site using a scraping motion of the hind legs. Digging was intermittent and between bouts the female would rest her throat on the soil atop the nest, or back off slightly and poke her snout into the hole. The muffled vocalizations of the young within the nest were heard from the beginning of the observations (2232 h).

The top of the first egg was visible at 2245 h, and the first hatchling was seen at 2249 h. To pick up hatchlings, the female would rotate her head laterally approximately 90 degrees, open her mouth, and gently grab at the hatchling with her jaws. Usually, several attempts were necessary to secure each young. Once she had picked up the hatchling, the female would flip it back into her gular pouch using an inertial feeding motion of the head and neck.

The further excavation of the nest and picking up of young was accompanied by the female giving occasional snorts, to which the young would respond by vigorously grunting. It was also noted from later examination of photographs that during this process the female

had everted her submandibular glands, suggesting that communication with the young may be both vocal and olfactory.

After collecting 4 hatchlings in her mouth, the female turned and leisurely walked down the incline in front of the nest and entered the water (2333 h). Once in the water she swam along the north shore of the breeding enclosure for a distance of 25 meters, then submerged. At 2335 h the female was seen at the surface swimming back along the same shore, and with the hatchlings still in her mouth, and climbed partially out of the water adjacent to the nest. The female continued swimming around the northern end of the enclosure until 2341 h, submerging once again with the hatchlings in her mouth. At 2341 h the female entered a grassy area along the waters edge 3 meters from the nest, and released the young.

During the next 5 hours the female made 6 more visits to the nest, carrying a total of 18 hatchlings from the nest into the water (distance=2 meters). During this time the male crocodile approached the nest site during the initial excavation process, but later moved off and spent most of the night near the center island in the enclosure. At 0317 h the male bellowed (2 jaw slaps/4 roars) but the female did not respond. The female was last seen on the nest at 0445 h, and the young were seen in a tight group in shallow water, or on shore near the nest site the following morning.

d. Parental Care

Both in captivity and in the wild, hatchling crocodiles remain together in a tight group, or "pod", for several weeks following hatching. Adult crocodiles with pods of hatchlings have been seen in the Rio Capanaparo (April 1987) approximately 1-2 weeks following hatching, as well as in the Rio Tucupido (April 1986), and the Camatagua reservoir (June 1986), approximately 3, and 4 weeks following hatching repectively. By the end of the following wet season, pods of crocodiles are no longer seen, suggesting that hatchlings disperse, or are heavily predated during the wet season. In neither the Rio Capanaparo nor the Camatagua reservoir did adult crocodiles remain with the pod upon our approach, even when the young began making "distress" calls when they were captured. This is in sharp contrast to reports of early explorers and indicates that crocodiles may have learned, or been heavily selected for, neutral defense behavior against humans.

Juvenile "distress" calls are similar in structure, but of greater intensity and higher pitch, to the "grunts" used for normal communication (Figure 6). Sound energy of grunts is principally below 2000 Hz, but the more structurally complex distress calls will attain 6000-7000 Hz. Although this species is notably less vocal than the sympatric *Caiman*, grunts probably play a role in inter-hatchling communication and the maintenance of pod cohesion. Distress calls may be important for attracting the attention of larger conspecifics, for instance when the hatchling is grabbed by a predator.

Under captive conditions at Hato Masaguaral, the hatchling pod remained quite cohesive during the 3.5 months they remained in the breeding enclosure. Pod cohesion was especially notable during the day, when the group could usually be seen basking together, frequently on or near the female. Approximately 3-4 weeks following hatching, the pod began to spread out at night, and at times could be seen evenly dispersed around the entire 20 m x 20 m lagoon. However, by the next morning the pod would once again be tightly grouped adjacent to the nest site. This pattern of activity continued until the hatchlings were removed from the breeding enclosure.

During the time the hatchlings were left inside the enclosure, the male and especially the female, were extremely vigorous in their defense of the young. Any approach to the vicinity of the nest site was usually met with the female rushing out of the water with an open mouth, and occasionally she would bite at the fence in an attempt to reach the intruder.

4.4. ECOLOGICAL INTERACTIONS

This section will deal with potential ecological interaction between Orinoco crocodiles and other species of crocodilians. At least three and possibly four species of crocodilians are sympatric with Orinoco crocodiles in various parts of the crocodile's range. These species will be dealt with individually and potential ecological interations suggested. In at least one species, Caiman crocodilus, these interactions may be significantly detrimental and play an important role in retarding crocodile population recovery.

4.41. American Crocodile

The American crocodile, Crocodylus acutus, is the only congener that may overlap the range of the Orinoco crocodile. As mentioned in section 1, the distribution of crocodiles within the potential range of overlap is virtually unknown. American crocodiles are known from as far east as the northern coast of the Paria Penninsula. Whether or not this species extends its range south into the Rio San Juan or into the Orinoco Delta is uncertain. Medem (1983) reports an unconfirmed record of C. acutus from the Rio San Juan. However, the one record from the Orinoco Delta is indicated to be C. intermedius. Hence the coexistence of the two species in one area cannot be positively demonstrated and any ecological interation today would be minimal.

4.42. Paleosuchus

Two species of Paleosuchus are found within the range of the Orinoco crocodile in Venezuela; P. palpebrosus, and P. trigonatus. Both species are small and inconspicuous, and their distribution in Venezuela is not well understood (Gorzula and Paolillo 1986). However, both species are known to occur in low densities in the states of Bolivar, Apure, and in Territorio Federal Amazonas. P. palpebrosus is also reported from Monagas state. Both species are usually restricted to river courses, ranging from large rivers to small morichales (Gorzula and Paolillo 1986), but they may also be found in artificial bodies of water such as the Guri reservoir (Gorzula, pers. comm.). Although usually found apart, there apparently are some cases where they may occur sympatrically (Medem 1967, Gorzula and Paolillo 1986). Gorzula and Paolillo (1986) noted an altitudinal separation with P. trigonatus being found in higher regions (up to 1,300 m).

P. palpebrosus is a very small species that has a widespread, but poorly understood distribution in Venezuela, and little is known concerning its habitat requirements (Gorzula and Paolillo 1986). Because of its scarcity and apparently patchy distribution, no good data on population density exist. This species may be broadly sympatric with Orinoco crocodiles in certain regions. However habitat requirements may keep the two species apart. For instance, in the Rio Capanaparo drainage, crocodiles are principally found in the main river channel or in sizeable tributaries. The P. palpebrosus, are only encountered in very small palm-lined creeks referred to as Morichales. In this situation there is little ecological overlap between the two species and interactions would be infrequent.

Although Gorzula et al. (in press) found hydrological differences in the habitat of Paleosuchus trigonatus and Orinoco crocodiles, P. trigonatus is not infrequently found in larger rivers where it may come into contact with crocodiles. Adult males have been found in the mainstream Rio Caura where a crocodile population is known to exist (pers. obs.). Reports by Godshalk (1982) indicate that this species is also found together with crocodiles in the Rio Cinaruco. However, in these situations, P. trigonatus is found in low densities. Gorzula and Paolillo (1986) report a mean density of 0.79/km in 10 rivers surveyed in the Guyanan region of Venezuela. Additionally, because so little is known about the ecology of this species, it is possible that a degree of habitat segregation occurs in areas shared with Orinoco crocodiles. Overall, the degree of ecological interaction with crocodiles is probably quite low.

4.43. Spectacled Caiman

The spectacled caiman (Caiman crocodilus) is the most widespread and abundant crocodilian in Venezuela. Based on historical accounts and interviews with old crocodile hunters, in the llanos prior to the commercial exploitation of the Orinoco crocodile, the caiman was not very abundant, and was found principally in isolated lagoons or small caños. Two subsequent events have resulted in a tremendous increase in llanos populations of Caiman: 1) the virtual extirpation of crocodiles from riverine habitats, and 2) the creation of many new permanent water habitats in the savannas associated with the expansion of the cattle industry and road construction.

Niche expansion of Caiman crocodilus has been reported from other parts of South America in relation to the decline of more commercially valuable crocodilian species: Melanosuchus niger in Brazil (Magnusson 1982), Caiman latirostris in Argentina (Muniz Saavedra 1983), or by colonization of newly formed aquatic habitats: (Magnusson 1982). In Venezuela, a similar situation exists with the virtual extirpation of the Orinoco crocodile (and American crocodile), and the creation of new permanent water habitats from the expansion of the cattle industry (creating watering sites for cattle), and road construction with the associated production of thousands of borrow pits that retain water year-round.

The opening of tremendous amounts of new habitat, combined with the high reproductive potential of Caiman as well as human tolerance for its presence has resulted in a great increase in Caiman populations over the last 50 years. Caiman now occupy virtually any sizeable body of water in the llanos including the rivers and caños, the former habitat of the crocodile. In some areas Caiman densities can reach prodigous levels. Dry season densities of non-hatchlings in some borrow pits may exceed $0.2/m^2$ (200/Ha). Likewise in rivers and reservoirs, Caiman density can be extremely high during the dry season. In the Rio Guarico, wet season density has been measured at 1.24/km (30 July 1986). The corresponding density during the dry season (8 March 1987) was 24.9/km, a 20 fold increase. Caiman densities have been noted to be equally high or higher in other

llanos rivers during the dry season: Rio Chirgua 52.3/km, Rio Orituco 22.2/km. In areas where reasonably dense crocodile populations are still found, Caiman densities are lower: Rio Capanaparo-7.27/km, Rio Tucupido-12.5/km. Likewise, Caiman densities in reservoirs are high, but do not change as much on a seasonal basis: Camatagua reservoir, low water-16.1/km, high water-12.6/km.

The high densities of Caiman in crocodile habitat may have negative effects on crocodile population recovery via two mechanisms: 1) ecological competition for limiting resources (food, preferred habitats), or 2) by the predation of larger Caiman on hatchling or young crocodiles. Little direct evidence of competition or predation between crocodiles and Caiman exists. Nevertheless, indirect inferences can be made based on the ecological data collected in this study, and the ongoing population study of Caiman on Hato Masaguaral.

4.431. Ecological Competition Few data exist indicating what, if any, ecological resources are limiting crocodilian populations, and what form interspecific competition may take. Former niche partitioning between crocodiles and Caiman was primarily along habitat lines. The crocodiles inhabited the rivers and larger caños, while the Caiman were relegated to the smaller, more ephemeral savanna wetlands.

Presently, in areas where low numbers of crocodiles still exist in rivers, they live among dense Caiman concentrations during the dry season. Once crocodiles reach adult size, they are larger and behaviorally dominant over Caiman. However, competition for resources may be occurring, especially among the smaller size classes. Perhaps the two most important resources under these circumstances are food and space.

If we define competition as the "use of a resource by an organism that thereby reduces the availability of the resource to others" (Ricklefs 1979), it is not difficult to imagine competition taking place under the dense dry season concentrations found in most llanos rivers.

The diet of virtually all hatchling and juvenile crocodilians is very similar, and is principally composed of aquatic or terrestrial invertebrates, especially insects. It would be quite reasonable to assume that juvenile Caiman and crocodiles would be eating the same prey items. Furthermore, the late dry season represents a time of reduced preyavailability and this would only serve to heighten competition.

Although a degree of habitat partitioning was found between Caiman and crocodiles in the Rio Capanaparo (see section 4.12), in situations with lower crocodile and higher Caiman densities one would assume a greater degree of overlap. Under these circumstances, large concentrations of Caiman would reduce preferred habitat availability for juvenile crocodiles.

4.432. Predation

Cannibalism is known to be a widespread phenomenon among Caiman in the llanos. Despite the active protection by the attending female, under high density situations, hatchling Caiman are frequently eaten by conspecifics, principally by larger juveniles or subadults. In fact, cannibalism may be one of the most important population regulating mechanisms in steady-state Caiman populations. Hatchling crocodiles are born in the late dry season or early wet season, when water levels are at their lowest and Caiman populations are the most concentrated. This combination of factors results in a high probability that in some areas, hatchling crocodiles will fall prey to Caiman.

No studies have been done of the food habits of Caiman in riverine habitats with crocodiles, so no direct evidence of Caiman predation exist. However, under similar circumstances in coastal Venezuela, direct evidence of Caiman predation on hatchling crocodiles has been found by A.E. Seijas of the Servicio Nacional de Fauna.

Some inferential data exists for direct interaction between crocodiles and Caiman. In certain areas where crocodiles and Caiman are found together, Caiman have an unusual response to the approach of a boat, they flee out of the water. In at least two populations, the Rio Capanaparo, and in the Caño Rabanal, Caiman will, on occasion, try to escape danger by vigorously running out of the water and up onto land. This unusual escape behavior may be an adaptive response to the presence of an aquatic predator, such as the crocodile. In areas where Caiman are not found together with crocodiles this behavior has never been observed.

In situations such as the Rio Capanaparo, and the Rio Tucupido, where reasonably dense crocodile populations still exist and a degree of habitat segregation can be seen, Caiman predation may be of secondary importance. However, crocodiles still exist virtually throughout their entire former distribution but at extremely low population levels, mostly consisting of adults. It has been previously assumed that, under these conditions, density levels were so low that animals could not encounter one another for reproduction (Godshalk 1982). However, it may be equally likely that crocodiles are reproducing amidst the dense Caiman populations, but that little or no recruitment is taking place due to severe first year mortality, in part caused by Caiman predation. Based on very preliminary evidence, this appears to be the case on the Camatagua reservoir, where reproduction is known to be taking place (Blohm 1982, this report), but little or no recruitment is seen.

5. FACTORS LIMITING CROCODILE POPULATION RECOVERY

Numerous factors are responsible for the failure of Orinoco crocodile populations to recover, despite the cessation of extensive commercial exploitation some 30 odd years ago. A clear understanding of these processes is of the utmost importance for planning a recovery program. Below is a discussion of what are currently recognized as the most important of these factors, segregated into those that can and cannot be directly related to human influence.

5.1 HUMAN-RELATED FACTORS

5.11 Continued Commercial Killing

Despite the collapse of the commercial hide industry in the late 1940's and 1950's, a limited amount of commercial killing still occurs, mostly on an opportunistic basis. Local people who live along river courses are usually very familiar with the crocodiles and where they may be found. Most are cognizant that a market still exists for skins, and if the opportunity presents itself, they will try to kill crocodiles for the hide. Illegal Caiman hunters of Colombian origin will also opportunistically take crocodiles (Godshalk 1982). The biggest market for hides is apparently through the Colombian town of Puerto Carreno (although some skins are still purchased in San Fernando de Apure). Hence, most of this commercial trade is from the Rio Meta, and to a lesser extent the Cinaruco.

5.12 Accidental Killing

Accidental killing principally occurs by drowning crocodiles in fishing nets. Illegal gill or seine nets are frequently used throughout the llanos in the dry season. Crocodiles are attracted to fish caught in gill nets, and will frequently become entangled and drown. Crocodiles accidentally caught in seines are usually killed, although recently some crocodiles have been removed alive to sell as pets.

In some instances crocodiles that have been accidentally drowned are skinned and the hides sold. This has been reported from the Rio Caura and the Capanaparo.

5.13 Deliberate Non-Commercial Killing

Crocodiles (especially adults) are often killed for a variety of other reasons: for "sport," because they represent a real or imagined threat to people or livestock, or simply for the sake of killing them. Certain crocodile by-products are occasionally utilized (e.g. teeth which are considered to have magical properties)

5.14 Subsistance Killing

The subsistence use of crocodile meat is not widespread in Venezuela. Among certain Indian groups, *Caiman* or *Paleosuchus* meat is readily eaten, but crocodiles are avoided. Although there are exceptions, campesinos do not eat crocodile meat either. However, in many areas crocodile eggs are considered a delicacy. During the early dry season, beaches are frequently checked for turtle eggs (*Podocnemis expansa*, *P. unifilis*), and when encountered, crocodile eggs will also be taken. Nest robbing is a major problem in the two largest crocodile populations, the Rio Capanaparo (pers. obs.), and the Rio Cojedes/Sarare (Godshalk 1978), and is widespread throughout the llanos (e.g. Rio Manapire).

5.15 Commercial Capture

Recently there has been an increase in the capture of crocodiles for sale to tourists or local ranchers. In certain areas such as the Rio Capanaparo, hatchling crocodiles are actively sought (mostly by Indians) for sale to tourists from San Fernando, or from the larger northern cities. This illegal commerce has been ongoing for at least a decade, but apparently has intensified in recent years.

Likewise, captured juvenile or adult crocodiles are now also being offered for sale, frequently at exorbitant prices. Adult crocodiles reportedly have been purchased by ranchers in Apure to keep in captivity on their property.

5.16 Habitat Deterioration and Destruction

The expansion of the human population and agricultural industry in the llanos has led to a certain amount of habitat deterioration and in some instances almost complete habitat destruction. Water pollution caused by town effluent or pesticide usage is a major, although unquantified, problem in several river drainages, most notably the Portuguesa and the Guarico. The Rio Cuchivero is also contaminated with runoff from several mining operations on the Rio Guaniamo, its principal tributary.

Outright destruction of crocodile habitat represents a grave threat to the Rio Cojedes/Sarare crocodile population. River channelization and the construction of irrigation canals will all but eliminate most of the riverine habitat in this area. Furthermore, this river is highly contaminated with sewage from the city of Barquisimeto, and pesticide runoff from the nearby Turen agro-industrial center (Ayarzaguena 1987).

Another form of human-related environmental alteration is the construction of reservoirs. The overall effect of creating reservoirs is uncertain, but in many respects it may be beneficial for the crocodiles. However, little is known about the effects on crocodiles downstream from the dam, and the lacustrine environments formed by damming a river do not create ideal crocodile habitat. Reservoirs usually lack sandy nesting beaches and do not have extensive shallow water habitats. These lacustrine habitats appear to better habitat for *Caiman* than for crocodiles. However, reservoirs may provide the best areas for initiating a crocodile reintroduction program (section 6).

5.2. BIOLOGICAL FACTORS

5.21 Ecological Replacement by Caiman

The ecological interactions between *Caiman* and Orinoco crocodiles were discussed in section 7 of the ecological study. Suffice it to say here that there exists a good possibility that the seasonally dense *Caiman* populations characteristic of most llanos river courses are having a significant effect in retarding crocodile population recovery. Two mechanisms may be at work, ecological competition for resources, or direct predation by *Caiman* on juvenile crocodiles. This problem may be lessened in areas where locally "dense" crocodile populations still exist and a degree of habitat segregation is found. However, throughout the vast majority of the range of the Orinoco crocodile, this species is found in extremely low densities, amidst a large population of *Caiman*.

5.22 Population Dynamics

Another biological phenomenon that may slow crocodile population recovery has to do with aspects of the crocodiles natural population dynamics. In some parts of the world where other endangered crocodile populations have been protected, population recovery has been very slow. This has been the case in southern Florida with the American crocodile (*C. acutus*)(Kushlan and Mazzotti 1982), as well as in northern Australia with the salt-water crocodile (*C. porosus*)(Messel et al 1981). This is in spite of the fact that most of the human-related mortality had been effectively controlled, and there was no ecological equivalent of *Caiman* to occupy the empty ecological niche. In both these cases a complex series of factors were probably involved in the slow recovery. But these examples indicate that population recovery in large, long-lived crocodilians is naturally a slow phenomenon, even under the best of circumstances. The elucidation of the mechanisms at work in these situations will have to await a better understanding of the population dynamics of crocodilians.

6. CONSERVATION AND MANAGEMENT RECOMMENDATIONS

6.1 SITE SPECIFIC CONSERVATION RECOMMENDATIONS

Recommendations concerning the conservation of Orinoco crocodiles must address the principal points outlined above: 1) amelioration of human-related crocodile mortality, 2) protection of habitat, and 3) reduction of non-human related mortality, especially in the hatchling and juvenile size-classes. Further points of critical importance are: 1) the continuation of research on crocodile ecology, and status surveys of known populations, and 2) addressing the public relations problems that will invariably stem from a plan designed to increase populations of large, potentially dangerous predators.

Because the conservation problems vary between areas, the following recommendations will be made on a population by population basis, starting with the most important area considered in this study, the Rio Capanaparo. Three other areas merit individual consideration: the Camatagua reservoir, the Rio Caura, and the Rio Tucupido. No consideration is given here to the Rio Cojedes/Sarare crocodile population, which is currently under investigation by Dr. Jose Ayarzaguena.

6.11 Rio Capanaparo

The Rio Capanaparo represents our best chance for saving an Orinoco crocodile population in its natural habitat. First priority should be given to this population in the development of a management and conservation program.

The lower sections of the Rio Capanaparo are to be included in the Parque Nacional Cinaruco-Capanaparo. The creation of this park by the Venezuela government should be strongly endorsed. Particular attention should be given to the protection of the riverine fauna in the Capanaparo, the Cinaruco, and their major tributaries. Besides Orinoco crocodiles, both rivers contain populations of endangered or threatened river turtles (Podocnemis expansa, P. unifilis), giant river otters (Pteronura brasiliensis), and river dolphins (Inia goeffrensis). The lower sections of both rivers may also harbor manatees (Trichechus manatus) on a seasonal basis.

However, the initial design of the park would only have included the lower sections of the Rio Capanaparo (to the boundary between Distritos Pedro Camejo and Achaguas in Apure). INPARQUES urgently needs to consider the extension of the park boundaries upstream at least to the level of Las Campanas. Although crocodiles are found throughout the Capanaparo, almost one half of the crocodiles below the confluence of the Rio Riecito are located in river section 3. River sections 2 and 3 (from Las Campanas to San Luis) together contain some 56% of the surveyed population. It is critical that this part of the river be included within the park, or offered some other form of legal protection.

Although inclusion of the Capanaparo in the national park will be a tremendous step forward, it will not in and of itself guarantee the

continued survival of the crocodile or other riverine fauna. Restrictions must be place on the excavation of crocodile eggs, and the capture of hatchling for sale. Together, these two factors are the most responsible for limiting crocodile population growth in the Capanaparo system. Another major source of crocodile mortality is drowning, or capture in fishing nets. Hence, restrictions on gill and seine netting will also need to be better enforced.

Continued monitoring of the crocodile population, as well as research on crocodile ecology, should be continued indefinitely. Much more needs to be known about this crocodile population so that we can formulate more specific conservation recommendations.

Towards accomplishing these goals, it is strongly urged that a biological station/guard house be established in the vicinity of the major crocodile concentration (e.g. Santa Rosa). This facility could be used to house Venezuelan students and biologists who would conduct studies on the fauna of the region. The station could be used as a base for the biologists to continue monitoring the crocodile population, collect crocodile eggs and hatchlings, as a center for environmental education, and also house park guards. If this region is considered for tourism, it could also serve as an overnight station for river cruises. The operation of such a station could be made a joint operation between an investigative branch of the government (e.g. the Servicio Nacional de Fauna) or a private foundation (e.g. FUDENA), and the National Parks Department (INPARQUES). Funds for the establishment of this station could be sought from international conservation organizations, or potentially though Venezuelan foundations or interested groups.

Among the duties that could be undertaken by personnel from the biological station would be:

1. Monitor crocodile populations.
2. Conduct ecological research.
   a. Crocodile population ecology.
   b. Crocodile nesting ecology.
   c. Caiman-crocodile ecological interactions.
   d. Studies of Pteronura, river turtles or other fauna.
3. Monitor and protect crocodile nesting beaches and collect eggs/hatchlings for captive rearing (see below).
4. Monitor the success of the crocodile reintroduction program (see below).
5. Provide environmental education for local residents and park tourists.

A further strong recommendation would be to begin a program of "headstarting" crocodiles. Crocodile eggs, or hatchlings could be collected from wild nests on the Capanaparo, and the young reared in captivity to an age of approximately 2 years. Rearing should be done in accredited centers (e.g. Hato Masaguaral, UNELLEZ, San Carlos (La Salle, or newly developed rearing facilities) using proven techniques. Once they have attained a length in excess of 70 cm TL, crocodiles can be re-released in the Rio Capanaparo at a size when survivorship is greatly increased, hence speeding population recovery.

Concurrent with the reintroduction of crocodile should be an education program designed to minimize potentially dangerous interactions between people and crocodiles. A campaign alerting the local residents and tourists about the dangers of swimming in areas where crocodile are present will be essential. Most residents of the region already are cognizant of the dangers, and rarely swim in the river. Likewise, most tourists that visit the region during the dry season bath in the small, clearwater tributaries where crocodiles are not present. However, clear measures must be taken to avoid the potentially disastrous consequences of human death resulting from crocodile attack.

An important ingredient in the success of this program will be the support and active involvement of the local people. The banks of the Capanaparo are inhabited by people who utilize crocodiles on a subsistence basis (Yaruro Indians), as well as by campesinos who do not see any need to increase the population size of a potentially dangerous animal. Education, as well as providing economic incentives will make the local people more receptive to the conservation program, and greatly increase its chances of success. Three potential alternatives for increasing local involvement are:

1. Employ local people as park guards. Besides helping the local economy, these people are very familiar with the region and usually have a good working knowledge of the fauna.
2. Instead of restricting the collection of eggs and hatchlings for food, or sale to tourists, regulate this trade though sale to the government. Hatchlings could be purchased by the government and then placed in captive rearing centers. Digging up eggs and sale of young to tourists should be prohibited, and other safeguards taken to prevent abuse of this system. But by providing an economic incentive to sell hatchlings through legal channels, this plan could effectively eliminate the two biggest problems that face the Capanaparo crocodile population (nest robbing and illegal sale of hatchlings), as well as provide a ready source of hatchlings for captive rearing operations.
3. Seek community involvement in the release program. Invite local leaders to preside over the initial crocodile restocking efforts. Especially important will be to invite local children to actively participate in the release of the crocodiles and participate in environmental education programs.

This conservation program should also be extended to the Rio Cinaruco where a much smaller crocodile population is found.

6.12 Camatagua Reservoir

A different set of problems are manifest in the Camatagua crocodile population. Direct human related killing of crocodiles is limited to occasional poaching of adult crocodiles by fishermen or local residents. However, crocodiles face severe environmental

problems related to the artificial habitat in which they are found. The reservoir is a sub-optimal habitat, lacking in shallow-water habitat or suitable nesting beaches. Moreover, the lacustrine environment appears to be more suitable for _Caiman_, and this species is found here in high densities.

Crocodile reproduction is occurring in Camatagua (see Section 4.321), but it appears juvenile mortality is very high, and little recruitment is taking place. Because there is little shallow-water habitat, hatchling crocodiles may be more vulnerable to aquatic predatory fish such as _Serrasalmus notatus_, or _Cichla ocellaris_. Likewise, small crocodiles may fall prey to _Caiman_, which are found there in high densities throughout the year, as opposed to seasonally as in the majority of llanos rivers.

The Camatagua reservoir is already under a form of official protection as a "Zona Protectora" to protect the watershed surrounding the reservoir. Consideration should be given to declaring this area a wildlife refuge for the protection of the crocodiles and other wildlife. Because the reservoir has only limited access, control of entry could be monitored by the national guard. Of equal importance would be a campaign to inform local residents of the endangered status of the crocodiles and measures being taken to protect them. As the reservoir is full of pirañas (_Serrasalmus_ sp.), little or no recreational use of the reservoir exists beyond sport fishing and limited bathing in one or two localities. Hence, a good potential exists to reduce future human-crocodile interactions.

The Camatagua reservoir provides a good opportunity to release captively reared, or captively bred, crocodiles. Because the reservoir is a highly perturbed environment and does not represent a "natural" population, the release of captively bred crocodiles of unknown geographic origin should have few potential negative effects. In contrast, natural populations such as the Rio Capanaparo may be locally adapted to their local environment and attempts should be made to ensure genetic purity.

Crocodile headstarting should be seriously considered for the Camatagua reservoir. Even though it does not represent a pristine environment, the Camatagua reservoir, and other reservoirs in the llanos and surrounding areas, may provide important sites for maintaining crocodile populations in the face of increasing pressures on the few remaining natural populations. Studies on crocodile ecology in reservoirs should be undertaken, and a population monitoring program started. If possible, these surveys should coincide with the nest hatching season (May) in order to collect hatchlings for rearing in captivity.

Serious consideration should also be given towards establishing crocodile release sites in other reservoirs within the natural range of the Orinoco crocodile. Candidate sites are: Rio Verde reservoir, Guarico reservoir, Tucupido reservoir, Rio Pao reservoir, Majaguas Reservoir, and the Guanipito reservoir. Another potential release site would be the Guri lake on the Rio Caroni. Although this is technically outside the former range of the Orinoco crocodile, it is still within the Orinoco basin and merits consideration.

6.13 Río Caura

The Rio Caura crocodiles are another isolated population inhabiting an atypical habitat. Population levels appear to be very low in this river, but the area is remote and the potential for recovery is good. Very little is known about the crocodiles in the Caura, and more surveys and ecological work are needed to formulate specific management recommendations. Nevertheless, crocodile headstarting should be initiated here as soon as possible. Every effort should be made to locate nesting areas and either protect the eggs or remove them for incubation at another site. Because a long trip will be necessary to reach a rearing center, and eggs are easily killed by movement, incubation in situ, or in a nearby beach would be preferable. The EDELCA hydrological station at Pie de Salto could perhaps be used as a base for providing logistical support. Once the eggs hatch, the young could be more safely transported to another site.

Because the Caura is sparsely populated, and the few inhabitants are generally cognizant of the dangers crocodiles represent, the potential conflicts stemming from a release program should not be too great. Nevertheless, as part of ecological studies and population monitoring, local residents should be informed of the reasons for undertaking a reintroduction program, and support enlisted in the form of locating nests and perhaps a hatchling purchasing scheme similar to the one proposed for the Rio Capanaparo.

Because of the great natural beauty of the Rio Caura region and its great potential for tourism, it should be considered as a site for a national park. Indeed, one operation near Maripa (Campamento Caurama) is already taking groups upriver in dugouts. Because the only access is by boat, or by landing on an airstrip at Pie de Salto, entrance to the region could be controlled and managed for protection of the wildlife resource. Development of the tourism potential of the area should be done (as Campamento Caurama has done) in conjunction with the Makititare Indian community.

6.14 Rio Tucupido

The crocodile population in the Rio Tucupido will shortly be faced with a severe environmental disturbance, the damming of the river to create a reservoir. As mentioned in section 3.433, the newly created lacustrine environment will provide a habitable, but less than ideal, environment for the crocodiles. This situation provides an excellent opportunity to study the effects of river damming on a resident crocodile population. The schedule for the dam closing is uncertain, but it may be as soon as the dry season of 1988. However, the adjacent Rio Bocono has already been dammed and will eventually join to form one large reservoir with the Tucupido. Surveys should begin as soon as possible to see if crocodiles are found in the Bocono reservoir, and estimate population size. Additional survey and ecological work should be undertaken in the Rio Tucupido before it floods, as well as during and after flooding. Students and staff of the nearby UNELLEZ university should be encouraged to take an active

conservation interest in this crocodile population, and establish a research plan involving regular population surveys and ecological studies.

Associated with the damming of the river will be an immediate deficit of water downstream from the dam site. Crocodiles have been reported from this area, so when the dam is closed, every effort should be made to locate and capture these crocodiles and 1) translocate them into the river upstream of the dam or 2) use them for breeding stock in captive propagation programs.

The captive breeding station for Orinoco crocodiles at UNELLEZ in Guanare is located very near to the Rio Tucupido crocodile population. This center could be used not only for captive propagation, but also as a rearing facility for hatchling crocodiles from wild nests along the Rio Tucupido. Funding for such work could be sought from international conservation organizations. In this respect the damming of the Rio Guarico to form the Camatagua reservoir may serve as a good example of what to expect with the Tucupido reservoir. The lack of shallow water habitat, nesting beaches, and poor recruitment into the breeding population may all act to limit the growth of the crocodile population in the reservoir. Under these circumstances, a restocking program with crocodiles raised at UNELLEZ would be a very appropriate management alternative. Another possibility would be the creation of nesting areas by landscaping shoreline regions to enhance nesting potential.

As a last measure, the Tucupido/Bocono reservoir should be given official protection as a wildlife sanctuary. Access to the area should be monitored by the national guard, and publicity generated (through the restocking program) to develop a positive local attitude towards crocodile conservation.

6.2 GENERAL RECOMMENDATIONS

The successful conservation of the Orinoco crocodile will depend on a program that rests on 4 basic cornerstones:

1. Ecological investigation and population monitoring
2. Education
3. Reintroduction of juvenile crocodiles
4. Protection of habitat and reduction of human-related mortality

The conservation program will of necessity be a multi-institutional effort involving the Venezuelan government, non-governmental organizations, and private individuals. An effort must be made to coordinate the development of this program from the start, and seek financial support to carry out its objectives. A meeting should be held at the earliest possible date, to decide upon a course of action.
The goal of this meeting should be to develop a coordinated national conservation plan that takes into consideration: protection of wild habitat, crocodile reintroductions, restocking and translocations, and other potential management alternatives. Conservation and

research priorities should be established, and a firm commitment should be sought from the government to adopt a recovery plan for the Orinoco crocodile.

Aside from the establishment formal recovery plan, and the population-specific recommendations outlined above, several additional recommendations can be made here with respect to the development of a conservation program.

Foremost is the need to develop a permanent source of funding for crocodile conservation. While the Venezuelan government and international conservation agencies can be counted on to fund much of the work, other sources are needed. One appropriate means of funding crocodilian work in general would be through the proceeds of the Caiman harvest. Caiman are abundant throughout the llanos region of Venezuela, and have been harvested on an experimental basis 4 of the last 5 years. A properly managed harvest can be sustained indefinitely and provide an economic basis for the conservation of the resource. Caiman skins are a valuable commodity on the international market and can provide Venezuela with foreign exchange. Some of these earning should be reinvested in management of Caiman, and likewise used for crocodile conservation. A general fund for crocodilian management and research could be established through a government imposed tax on hides. Similarly, interest has been expressed by hide producers (llanos land owners), and Venezuelan tanners in establishing an association tentatively called ASOBABA. Organizers have expressed interest in imposing a tax on members to fund research on Caiman and other crocodilians. Support should be given towards the establishment of this organization, and the development of a fund for crocodile research.

The second general recommendation is to expand facilities for the captive rearing of hatchling crocodiles. More emphasis should be placed on collecting eggs from wild nests, rearing the hatchlings to a size of 1-1.2 m total length, and releasing them in their population of origin. Currently there are two operational captive breeding/rearing centers for Orinoco crocodiles: at Hato Masaguaral, and at the UNELLEZ facility in Guanare. These operations should be expanded and used for rearing wild produced crocodiles as well. Additionally, in conjunction with the collection of eggs or hatchlings from other crocodile populations, additional captive rearing centers should be established. The most cost effective approach would be to use facilities at zoos, remodeled according to suggestions by personnel from operational rearing centers. The installations at the Parque Loefling in Puerto Ordaz, and some of the zoos in Caracas, Maracay, Valencia and Barquisimeto are among the potential sites that could be used. The use of zoos in major cities would have the additional benefit of providing excellent opportunities for public education on a widespread level.

The last general recommendation is to begin an intensive public education campaign. Public education should be done at two levels: addressing the general public throughout the country, and also to work more intensively with people in areas where reintroductions are contemplated. As mentioned previously, the captive rearing of crocodiles in public zoos in some of the major cities will provide opportunities to increase public awareness of the plight of the Orinoco crocodile and other endangered species. Governmental and

private organizations should work together to develop a broad-reaching educational campaign designed to increase public understanding of conservation problems, and what is being done to resolve them.

Education at the local level should also focus on the theme of living together with crocodiles. Emphasis should be given to the fact that the crocodiles are a national heritage, an effort made to develop a local sense of pride in having a crocodile reintroduction program. In this sense it would be beneficial to involve local communities as much as possible in the actual reintroductions (e.g. invite community leaders and local residents, especially children) to actively participate in the release of juvenile crocodiles.

The last general recommendation is to continue research into basic aspects of the ecology of the Orinoco crocodile. Our present understanding of the natural history of this species is at best minimal. Particular importance should be placed on seasonal habitat usage and patterns of movement, nesting ecology, juvenile survivorship, and ecological interactions with Caiman. Before any reintroductions or restocking are started, detailed information should be gathered on the crocodile and Caiman populations at the release site. Detailed follow-up programs involving regular censuses and radio-telemetry should be made to assess the effectiveness of the release programs.

7. SUMMARY

1. Population Status

Crocodile populations continue to remain extremely depleted throughout Venezuela. Little or no population recovery has taken place in any part of Venezuela. A larger total crocodile population estimate can be made than was previously thought (e.g. Godshalk's estimate of 1,000 wild animals (IUCN 1983)), but this is based primarily on more detailed surveys of known populations, or the discovery of new ones. Based on the results of this study, only three populations can be said to have more than 50 non-hatchling crocodiles: the Rio Capanaparo and its tributaries (estimated population 400-500), the Embalse de Camatagua (>50), and the Rio Tucupido (100). Several other crocodile populations may number more than 50, but more survey work needs to be done to confirm this. Among these rivers are: the Rio Cinaruco, the Caura, the Ventuari, and the Manapire. One other crocodile population, that of the Rio Cojedes/Sarare region of Cojedes/Portuguesa state is known. This crocodile population, which may be the largest remaining concentration of Orinoco crocodiles, is currently under investigation by Dr. Jose Ayarzaguena of the Fundacion LaSalle de Ciencias Naturales.

2. Ecology

Habitat Relations--Orinoco crocodiles were widely distributed throughout the Orinoco river drainage, but reached their greatest abundance in the lower llanos sections of the large, turbid rivers such as the lower and middle Orinoco, or tributaries draining the Andes and the Coastal mountain range (type Ia tributaries). The Orinoco tributaries with the largest crocodile populations were the Rio Guaviare-Guayabero and the Rio Meta systems in Colombia, and in Venezuela the Apure-Portuguesa system, and the Rios Arauca, Capanaparo, and Guarico-Guariquito. The middle and upper sections of type Ia tributaries also contained seasonally dense crocodile populations. Two of the largest remaining crocodile populations are located in the upstream (Rio Cojedes-Sarare) and piedmont (Rio Tucupido) sections of type Ia tributaries. Less dense crocodile populations were found in the clearwater, internal llanos drainage systems such as the Vichada in Colombia, and the Cinaruco, and Cuchivero in Venezuela (type Ib tributaries).

Crocodiles were also found in much lower densities in the Guayanan shield clearwater rivers (type IIb) such as the Ventuari, and the Cuchivero. No reports of crocodiles are known from the Rio Caroni, a large blackwater tributary (type IIa) of the lower Orinoco. However, a small population of crocodiles is found in the nearby Rio Caura, which has characteristics of both IIa and IIb rivers.

The present distribution of surviving crocodile populations should not be viewed as representative of the species' historical distribution. Rather these populations remain principally in isolated regions where past hunting, and continued human population

pressures have not resulted in local extirpation, and hence are biased against the downstream type Ia river sections where human development pressure has frequently been the most intense.

Crocodile microhabitat selection was investigated primarily in the Rio Capanaparo during the dry season. The Capanaparo represents the largest crocodile population remaining in what was formerly the most characteristic crocodile habitat; the lower and middle sections of type Ia rivers. Within the Capanaparo, crocodiles showed definite preference for certain areas. Crocodiles reached their highest density in sparsely populated regions of upstream river sections. Few crocodiles were observed in the lower river region due to human predation pressure and increased crocodile wariness. Upstream, crocodiles showed an evident preference for the broad, sandy stretches of river that had extensive beaches and a mixture of shallow/sandy areas and deep water. River bends and the downstream sides of mid-channel bars, (especially where mid-channel sandbars formed adjacent to deep pools) were particularly favored. During the morning (0830-1100 h), an estimated 20% of the crocodiles >2.0 m TL were out basking. Basking crocodiles showed a preference for sandbar islands.

Nocturnal surveys revealed crocodiles preferred open, sandy river stretches with a low shoreline gradient, and avoided the straight river segments lined with trees and shrubs. Juvenile crocodiles preferred shallow water areas near the shore, whereas adults were usually seen in open water >5 m from the shore. Sympatric *Caiman* were almost invariably associated closely with the shoreline, normally in more heavily vegetated areas, and frequently along shores with steep gradients. Oxbow lakes provided good *Caiman* habitat, but recently formed oxbows were also used by adult crocodiles. Juvenile crocodiles were never seen outside of the main river channel.

In other habitats, such as Andean piedmont streams (Rio Tucupido), small intermittent llanos rivers (Rio Orituco), or Guayanan shield tributaries of the Orinoco (Rio Caura), crocodiles occupied deep water sections of the rivers, and if water stressed, would construct burrows along undercut riverbanks or shores with sharp dropoffs. Burrows apparently serve as diurnal refuges, or aestivation sites for one or several crocodiles during the dry season.

Crocodiles also inhabit reservoirs in piedmont and llanos habitat in Venezuela. The lacustrine environment formed by damming rivers creates sub-optimal crocodile habitat lacking extensive shallow water habitat (especially in piedmont regions), and open sandy beaches. Adult crocodiles in the Camatagua embalse use floating mats of vegetation as resting and basking sites. Few or no juvenile crocodiles have been observed in these habitats.

Population Ecology--Crocodile populations throughout most of Venezuela are extremely diffuse. Only two riverine populations with reasonably high population densities were encountered. Based on aerial surveys, corrected non-hatchling population densities for the Rio Capanaparo in Apure State averaged 0.81/km, with the highest value being 4.10/km in river section 3 (25 km long). Corrected noctural boat surveys on river section 3 produced a similar estimate of 4.56/km. Hatchling density shortly after nest opening was 2.96/km.

In the Rio Tucupido, a small piedmont river, combined juvenile and adult density was estimated to be 3.44/km. In the majority of other rivers surveyed, corrected crocodile densities would be well below 0.1/km.

The population size-class distribution in the Rio Capanaparo shows a relatively healthy population with 38.5% juveniles, 21.3% subadults, and 35.0% adults. Based on population density, the size-class distribution, and a length-weight regression, biomass was estimated to be 39.2 kg/km overall, and 197.8 kg/km in the densely populated section 3.

The crocodile population in the Rio Tucupido appears to be somewhat truncated, and has no large crocodiles. Juveniles composed 84.6% of this population, and only 15.4% of the crocodiles were over 2.0 m TL.

Growth rate data comes mostly from captive animals. Hatchlings and yearlings normally grow 0.02-0.06 cm SVL/day, but individual animals have been known to grow up to 0.075 cm SVL/day. Larger juveniles and subadults can maintain these growth rates at least up to an age of 7 years. Age at sexual maturity may be as little as 7-9 years in females, and 9-11 years in males.

The few data on growth rates of young juvenile crocodiles in the wild suggest that these may vary considerably between populations. Hatchlings and yearlings on the Rio Capanaparo grow 0.06-0.08 cm SVL/day, whereas young from the Tucupido only grow 0.03 cm SVL/day.

Reproductive Ecology--The courtship and nesting period for Orinoco crocodiles extends from late September to February, peaking in December and January. The male's advertisement display (AD) consists of a combination of jaw slaps (mean=1.93) and roars (mean=3.39), given from a head elevated, tail elevated posture in shallow water. The AD may be given at any time of the year, but peaks in January. Twenty-four hour observations show a diurnal peak in the AD just before dawn.

Courtship consists of a series of sterotyped behaviors including slow swimming in circles, snout rubbing, bubbling, and repeated submergences. Copulations were seen from late November to early January.

Nesting occurs in the early dry season, January and February, and hatching in March through May. Some evidence suggests that nesting schedules may change depending on the hydrological cycle of the river in order to ensure hatching before the wet season floods.

Eggs are laid in holes, usually dug into sand beaches along rivers, but nests may be found in a variety of soil substrates. The nesting behavior of a captive female is described. Nest holes are normally 45-65 cm deep, with the top of the eggs buried 25-45 cm below the surface. Clutch size in the Rio Capanaparo ranged from 21 to 65 (mean=48). Egg fertility was high (97%). Incubation usually lasts 80-90 days. At the end of incubation the female will excavate the nest and carry the young to the water. Hatchlings remain grouped together in pods for at least one month after hatching, but disperse during the rainy season. Adult protection of nests and young is minimal today, but was much more widespread in past times.

Ecological Interactions--The range of the Orinoco crocodile overlaps those of 4 other crocodilians: *Crocodylus acutus*, *Paleosuchus trigonatus*, *P. palpebrosus*, and *Caiman crocodilus* . Ecological interactions between Orinoco crocodiles and these other species are negligible with the exception of *Caiman*. Strong circumstantial evidence suggests that the recent expansion of *Caiman* populations into former crocodile habitat may be an important factor retarding crocodile recovery. Two mechanisms are viewed as being important in this regard: direct interspecific predation, and ecological competition.

3. Factors Limiting Population Recovery

Human-related and biological factors that may be responsible for impeding crocodile population recovery are analyzed. Potential factors include:

1. Continued commercial killing of crocodiles for their skins
2. Accidental killing
3. Deliberate non-commercial killing
4. Subsistence use of eggs
5. Capture for sale to tourists, or local landowners
6. Habitat deterioration or destruction
7. Ecological replacement by *Caiman*
8. Intrinsically slow population recovery

Some or all of these factors may be operating to varying degrees throughout the range of the Orinoco crocodile. The order of importance appears to be different depending on local circumstances. For instance in the Rio Capanaparo, the most important factors appear to be 4 and 5, subsistence use of eggs, and the sale of hatchlings to tourists. The remnant population in the Rio Cojedes/Sarare appears to be most threatened by habitat destruction. However, in areas of extremely low crocodile density, ecological replacement by *Caiman* may be of overriding importance.

4. Conservation Recommendations

A series of population specific and overall recommendations for the conservation of the Orinoco crocodile in Venezuela are made.

General Recommendations

1. Develop a formal recovery plan for the Orinoco crocodile. The plan needs to be actively supported by the Venezuelan government, and planned and carried out in conjunction with interested non-governmental organizations.

2. Generate additional sources of funding for implementing the recovery plan. One possible approach would be to use revenue from the Caiman harvest, either through the government, or a private association of tanners and ranchers.

3. Expand captive rearing facilities for crocodile reintroduction and restocking programs. More emphasis needs to be placed on the collection of wild-produced eggs or hatchlings for later release back into their source population.

4. Intensify public education on the national level, and locally in areas where active crocodile conservation management is contemplated.

5. Continue or expand the ongoing research on crocodile population status and ecology.

Population Specific Recommendations

1. Rio Capanaparo

   a. Extend the park boundaries upstream along the Capanaparo to include the major crocodile concentration. The river should be protected at least up to the level of Las Campanas.

   b. Enforce the restriction on illegal sale of hatchling crocodiles and the consumption of eggs.

   c. Initiate a government-coordinated program to purchase hatchlings from indigenous residents. The hatchlings would be transported to a rearing center and used to restock the Capanaparo when ca. 2 years of age.

   d. Establish a combination biological station-park guard house in the vicinity of Santa Rosa to:

      i. conduct studies of crocodiles and other riverine fauna, monitor population levels.
      ii. protect crocodile/turtle nesting beaches
      iii. facilitate tourism
      iv. provide environmental education

2. Camatagua Reservoir

   a. Protect the aquatic environments as a wildlife refuge.
   b. Collect hatchling crocodiles and rear for later restocking.
   c. Identify other reservoirs where similar conservation measures can be taken.

3. Rio Caura

   a. Obtain official protection for Caura region as a national park.
   b. Collect hatchling crocodiles and rear for later restocking.

4. Rio Tucupido

   a. Establish a research program through UNELLEZ to monitor and study the Tucupido crocodile population.
   b. Continue UNELLEZ captive breeding work, and expand to rearing wild produced hatchlings for restocking into the reservoir.
   c. Declare reservoir a wildlife sanctuary and develop a public education campaign centered on the restocking program.

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Table 1. Major Colombian rivers and their tributaries known to have at one time contained populations of *C. intermedius*. Indendented rivers are tributaries of previous non-indented river (from Medem 1981).

- Arauca
- Capanaparo
- Cinaruco
- Cano Cinaruquito
- Meta
  - Cravo Norte
  - Casanare
  - Cano Lipa
  - Cano Aguaclara
  - Cano La Candelaria
  - Cano de la Hermosa
  - Guachiria
  - Cano Gandul
  - Cravo Sur
  - Cusiana
  - Upia
  - Manacacias
  - Vita
  - Cano Verde
  - Pauto
  - Chire
  - Ariporo
  - Guanapalo
- Yatea
- Toma
  - Cano Gavilan
- Tuparro
- Vichada
  - Muco
  - Planas
  - Guarrojo
  - Tiaba
  - Uva
- Guaviare
  - Inirida
    - Cano Grande
  - Ariari
    - Cunimia
    - Guejar
  - Guayabero

Table 2. Summary of aerial survey for Orinoco crocodiles in Venezuelan Rivers: 1986-7. Uncorrected density values.

River	Date	Linear River Distance (km)	# Crocodiles Seen	Density (/km)
Region: Llanos				
Orinoco	17/19 Apr 86	560	0	0.000
Arauca	18 Apr 86	335	0	0.000
	31 Mar 87	9	1	0.111
Capanaparo	18/19 Apr 86	445	39	0.088
	01 Apr 87	78	17	0.218
	14 Apr 87	158	31	0.196
	16 Apr 87	142	12	0.085
	17 Apr 87	247	43	0.174
Riecito	16 Apr 87	84	2	0.023
Cinaruco	19 Apr 86	365	2	0.005
	14 Apr 87	210	0	0.000
Claro	16 Apr 87	50	0	0.000
Manapire	21 Apr 86	50	0	0.000
Rio Aguaro	21 Apr 86	40	0	0.000
C. Caballo	21 Apr 86	45	1	0.022
Region: Bolivar State				
Caura	16 Apr 86	270	4	0.016
Cuchivero	15 Apr 87	210	0	0.000
Region: Piedmont				
Tucupido	19 Apr 86	31	4	0.129
	20 Apr 86	31	19	0.613

Table 3. Aerial Survey Summary for the Rio Capanaparo: April 1986. Uncorrected density values.

River Section	Linear Distance (km)	# Crocodiles Seen	Density (#/km)
Cano Cubarro-El Porvenir	165	0	0.000
El Porvenir-Sta Rosa	60	6	0.100
Sta Rosa-San Pablo	105	15	0.143
San Pablo-Santa Ana	60	18	0.300
Santa Ana-Rio Orinoco	55	0	0.000

Table 4. Aerial Survey Summary for the Rio Capanaparo: April 1987. Uncorrected density values.

River Section	Date	Linear Distance (km)	# Crocodiles Seen	Density (#/km)
1)Rio Riecito-Las Campanas	1 April	47	3	0.064
	14 April	47	3	0.064
	17 April	47	4	0.085
2)Las Campanas-Cano Amarillo	1 April	16	2	0.125
	14 April	16	8	0.500
	17 April	16	3	0.188
3)Cano Amarillo-San Luis	14 April	25	14	0.560
	17 April	25	22	0.880
4)San Luis-El Naure	14 April	20	3	0.150
	17 April	20	4	0.200
5)El Naure-Casanarito	14 April	38	3	0.079
	17 April	38	4	0.105
6)Casanarito-El Betun	14 April	12	0	0.000
	16 April	12	3	0.250
	17 April	12	1	0.083
7)El Betun-San Pablo	16 April	22	3	0.136
	17 April	22	2	0.091
8)San Pablo-Macanilla	16 April	18	2	0.111
	17 April	18	3	0.166
9)Macanilla-La Pica	16 April	53	4	0.075
	17 April	53	0	0.000
10)La Pica-Orinoco	16 April	37	0	0.000

Table 5. Estimated number of crocodiles seen during 1987 aerial surveys of the Rio Capanaparo. Estimates based on corrections for 1) size-class, and 2) size-class and location.

River Section	Max. # crocodiles seen/size class 1-2m	2-3m	3-4m	4m+	Est. 1	Est. 2
1	1	2	3	0	6	7
2	3	2	3	0	8	10
3	4	9	9	0	22	32
4	0	3	1	1	5	5
5	1	1	2	1	5	6
6	0	1	2	0	3	4
7	1	2	1	0	4	5
8	0	1	2	0	3	5
9	0	2	1	1	4	4
10	0	0	0	0	0	0

Table 6. Corrected 1987 crocodile density (crocodiles per kilometer) values for the Rio Capanaparo, using 3 different correction methods.

River Section	Max. # Seen	Size-class Corrected	Size/Location Corrected
1	0.085	0.128	0.149
2	0.500	0.500	0.625
3	0.880	0.880	1.280
4	0.200	0.250	0.250
5	0.105	0.132	0.158
6	0.250	0.333	0.333
7	0.136	0.136	0.227
8	0.167	0.167	0.278
9	0.075	0.075	0.075
10	0.000	0.000	0.000

Table 7. Nocturnal spotlight counts of non-hatchling crocodiles (<1.5 meters, >1.5 meters total length, and "eyes only"/crocodile, EO/C) in river section 3 (25 km) and adjacent oxbox lakes, Rio Capanaparo, 1987.

Sublocale	Date	Total Non-hatchlings <1.5m	>1.5m	EO/C	Density (/km) <1.5m	>1.5m
River	23-28 Feb	7	12	.9	0.280	0.084
	29-30 Apr	15	21	5	0.600	1.040
Oxbows	23-28 Feb	0	3	5	0.000	1.636

Table 8. Estimated non-hatchling crocodile population size in the Rio Capanaparo, by river section (seetext for formulae). Observed number ofcrocodiles is mean for each section.

River Section	Number Aerial Surveys	Observed # Crocodiles >2 m	1-2m	Estimated # Crocodiles >2m	1-2m	Total Pop. Estimate	Density (/km).
1	3	3.00	0.33	11.11	2.75	18.48	0.39
2	3	3.33	1.00	12.33	8.33	27.55	1.72
3	2	14.00	3.00	51.85	25.00	102.47	4.10
4	2	3.50	0.00	12.96	0.00	17.28	0.86
5	2	3.00	0.50	11.11	4.17	20.37	0.54
6	3	1.33	0.00	4.93	0.00	6.57	0.55
7	2	1.50	1.00	5.56	8.33	18.52	0.84
8	2	2.50	0.00	9.26	0.00	12.35	0.69
9	2	2.00	0.00	7.41	0.00	9.88	0.19
10	1	0.00	0.00	0.00	0.00	0.00	0.00
Total						233.47	0.81

Table 9. Observed and estimated population size in the Rio Capanaparo river section 3, based on nocturnal spotlight counts and size-class specific correction values (P) from Bayliss et al 1986.

Size-class (m)	# Observed Crocodiles	P	# Estimated Crocodiles
0.5-1.0	9	0.745	12.12
1.0-1.5	6	0.765	7.82
1.5-2.0	4	0.733	5.12
2.0-2.5	3	0.585	5.12
2.5-3.0	6	0.325	18.52
+ 3.0	8	0.153	52.32
EO/C	5	0.383	13.0
Total	41		113.9

Note - P value for EO/C crocodiles was estimated by averaging P for all size classes greater than 2 meters.

Table 10. Total non-hatchling crocodile population estimate for the Rio Capanaparo basin in Venezuela.

Population Segment	Estimated Total
1. Rio Capanaparo-	
a. Orinoco-Riecito	233
b. Riecito-border	76
2. Rio Riecito	71
3. Oxbow lakes	23
4. Cano Tributaries	40
TOTAL	443

Table 11. Frequency of crocodile position categories recorded during aerial surveys, Rio Capanaparo and Rio Riecito, 1987. OS-On Shore, SWOE-shallow water on Edge, IW-In Water.

Date/Location	Time	OS Bar/Shore	SWOE Bar/Shore	IW
1 April Capanaparo	0840-1001	9/9	0/0	0
14 April Capanaparo	0830-1025	14/12	0/2	0
16 April Capanaparo	0831-1000	1/5	2/1	3
17 April Capanaparo	0839-1054	16/11	6/4	4
16 April Riecito	1606-1640	0/0	1/1	0
Total		40/37 39.6%/36.7%	9/8 8.9%/7.9%	3 6.9%

Table 12. Summary of observed crocodile and *Caiman* situations, main river channel and oxbow lakes, Rio Capanaparo. Percentage of total sightings based on nocturnal censuses 23-28 February 1987.

Situation	Caiman River	Caiman Oxbows	Crocodile River	Crocodile Oxbows
	(n=80)	(n=100)	(n=26)	(n=8)
On shore	40.0	7.0	0.0	0.0
Dead trees	18.8	19.0	3.8	0.0
In vegetation in water	3.8	12.0	0.0	0.0
Shallow water on edge	22.5	14.0	3.8	0.0
In water: <1 m	7.5	23.0	7.7	12.5
1-5 m	7.5	24.0	19.2	25.0
>5 m	0.0	1.0	65.5	62.5
Total	100.0%	100.0%	100.0%	100.0%

Table 13. Shore conformation adjacent to crocodiles and Caiman observed less than 5 meters from shoreline. Rio Capanaparo, main channel and oxbow lakes. Shore gradient. Based on noctural censuses 23-28 February 1987.

Shoreline Gradient	Caiman River (n=78)	Caiman Oxbow (n=97)	Crocodiles River (n=9)	Crocodiles Oxbow (n=3)
Steep	74.4	66.0	0.0	66.79
Moderate	3.8	10.3	0.0	33.39
Low	21.8	23.7	100.0	0.0
Total	100.0%	100.0%	100.0%	100.0%

Table 14. Shore conformation adjacent to crocodiles and Caiman observed less than 5 meters from shoreline. Rio Capanaparo, main channel and oxbow lakes. Shoreline Vegetation. Based on nocturnal censuses 23-28 February 1987.

Shoreline Vegtation	Caiman River (n=77)	Caiman Oxbow (n=103)	Crocodiles River (n=9)	Crocodiles Oxbow (n=3)
Aquatic Vegetation:				
Herbaceous	0.0	10.7	0.0	0.0
Live woody	0.0	0.0	0.0	0.0
Dead woody	0.0	0.0	0.0	0.0
No Aquatic Vegetation:				
Bare Shore	63.6	3.8	100.0	33.3
Shrubs	1.3	12.6	0.0	33.3
Forest	0.0	14.6	0.0	0.0
Overhanging forest	35.1	58.3	0.0	33.3
Total	100.0%	100.0%	100.0%	100.0%

Table 15. Shore conformation adjacent to crocodiles and Caiman observed less than 5 meters from shoreline. Rio Capanaparo, main channel and oxbow lakes. Shoreline Soil Type . Based on nocturnal censuses 23-28 February 1987.

Soil Type	Caiman River (n=75)	Caiman Oxbow (n=90)	Crocodiles River (n=9)	Crocodiles Oxbow (n=3)
Sand	28.0	6.7	100.0	0.0
Rock/pebble	0.0	0.0	0.0	0.0
Organic	72.0	93.3	0.0	100.0
Total	100.0%	100.0%	100.0%	100.0%

Table 16. Size-structure of Orinoco crocodile populations based on aerial and nocturnal spotlight censuses.

Nocturnal censuses

Location / Date	Size-class (m) 0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0+
Rio Tucupido	9	2	0	1	1	0	0	0
April 1986	69.2%	15.4%	0.0%	7.7%	7.7%	0.0%	0.0%	0.0%
Rio Capanaparo	3	4	3	5	2	3	1	0
Feb. 1987	14.3%	19.0%	14.3%	23.8%	9.5%	14.3%	4.8%	0.0%
April 1987	9	6	4	3	6	7	1	0
	25.0%	16.7%	11.1%	8.3%	16.7%	19.4%	2.8%	0.0%
Capanaparo	12	10	7	8	8	10	2	0
Combined	21.0%	17.5%	12.3%	14.0%	14.0%	17.5%	3.5%	0.0%

Aerial Censuses

Location / Date	Size-class (m) 1.0-2.0	2.0-3.0	3.0-4.0	4.0+
Rio Caura	2	2	0	0
April 1986	50.0%	50.0%	0.0%	0.0%
Rio Capanaparo	22	14	2	0
April 1986	57.9%	36.8%	5.3%	0.0%
April 1987	14	39	42	3
	14.3%	39.8%	42.9%	3.1%
Rio Tucupido	13	6	0	0
April 1986	68.4%	31.6%	0.0%	0.0%
Embalse de Camatagua	6	6	1	0
April 1986	46.1%	46.1%	7.7%	0.0%
March 1987	0	3	2	1
	0.0%	50.0%	33.3%	16.7%
Camatagua	6	9	3	1
Combined	31.6%	47.4%	15.8%	5.3%

Table 17. Average growth rates for 11 captive-reared female Orinoco crocodiles hatched in 1978. Measurments taken 2 June 1985. SVL= Snout-vent length, TL=Total length. TL values in parentheses are missing tail tip.

Crocodile	Crocodile Length (cm) SVL	TL	Average Growth Rate (cm/day) SVL	TL
HM-4	95.3	(127.0)	0.031	-----
HM-5	101.0	(179.5)	0.033	-----
HM-6	85.5	153.3	0.027	0.048
HM-7	120.5	(218.0)	0.041	-----
HM-8	109.4	200.5	0.037	0.066
HM-9	111.4	(204.6)	0.037	-----
HM-10	100.8	(177.0)	0.033	-----
HM-11	116.5	214.0	0.039	0.071
HM-12	120.5	(219.2)	0.041	-----
HM-13	115.0	210.3	0.039	0.070
HM-14	110.1	(199.5)	0.037	-----
Mean			0.036	0.064
Standard Deviation			0.004	0.011

Table 18. Growth records for a captive reared male Orinoco crocodile from Pto. Paez (Apure State) reared by Sr. Tomas Blohm. Hatching date April-May 1971.

Date	Total Length (cm)	Growth Increment (cm)	Age	Growth Rate (cm TL/day)	Accumulative Growth Rate (cm TL/day)
Jun 1972	58.5	28.5	1yr+1mo.	0.072	0.072
Oct 1973	72.0	13.5	2yr+5mo.	0.026	0.047
Nov 1977	184.0	112.0	6yr+6mo.	0.075	0.065
Jun 1980	220.0	36.0	9yr+1mo.	0.038	0.057
Nov 1984	285.0	65.0	13yr+6mo.	0.040	0.052
Mar 1987	314.0	29.0	15yr+10mo.	0.034	0.049

Table 19. Estimated crocodile biomass values for the Rio Capanaparo, river section 3 and the entire river downstream of the Rio Riecito. Estimated mass based on relationship $\log_{10}$ mass= $3.16(\log_{10}$ SVL$)-1.94$.

Size-class (m TL)	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	EO/CE
Frequency	21.95	14.63	9.76	7.32	14.63	17.07	2.44	12.20
Midpoint SVL (cm)	37.5	62.5	87.5	112.5	137.5	162.5	187.5	150.0
Predicted Mass (kg)	1.08	5.43	15.73	34.81	65.62	111.25	174.8	86.39
Estimated Population:								
Sect. 3	22.4	14.9	10.0	7.5	14.9	17.4	2.5	12.4
Sect. 1-10	51.1	34.1	22.3	17.1	34.1	39.8	5.7	28.4
Calculated Biomass: (kg)								
Sect. 3	24.2	80.9	157.3	261.1	977.7	1935.8	437.2	1071.2
Sect. 1-10	55.2	185.1	357.7	593.9	2237.0	4424.4	995.0	2453.5

Estimated Total Biomass:
River section 3 - 4945.4 kg (197.8 kg/km)
River sections 1-10 - 11301.8 kg (39.2 kg/km)

Table 20. Characteristics of six Orinoco crocodile nests found along the Rio Capanaparo in 1987.

Nest Parameter	Nest Number 1	2	3	4	5	6
1-Nest Type:	Bar	Bar	Playa	Bar	Playa	Playa
2-Distance to water (m):	9.5	10.3	16.5	6.0	10.0	5.0
3-Height above river (m):	4.19	4.16	3.98	3.09	2.85	2.40
4-Nest Depth						
top (cm):	-	45	38	25	-	-
bottom (cm):	-	64	62	45	(55)	-
5-Clutch Size:	-	65	58	21	-	-
6-Clutch Mass (g):	-	8017	6999	2386	-	-
7-Mean Egg Size						
length (cm):	-	7.77	7.78	7.96	-	-
width (cm):	-	5.15	4.93	4.80	-	-
mass (g):	-	123.3	120.7	113.6	-	-
9-Mean Hatchling Mass (g):	-	86.3	85.4	75.1	-	-
10-Egg Mass/ Hatchling Mass:	-	0.70	0.71	0.66	-	-
11-Egg Fertility:	-	96.9%	100.0%	95.2%	-	-
12-Soil % Water:	-	2.8%	3.2%	4.5%	-	-

Table 21. River level data for the Rio Orinoco and some major tributaries, February-May, 1978-1984. Values are for: a) mean maximum recorded water level, b) standard deviation in maximum recorded water levels, and c) change in water level from month x to x+1. All units in meters.

River (Location)		Feb		Mar		Apr		May
Rio Orinoco (Caicara)	a.	24.60	a.	24.50	a.	27.41	a.	30.82
	b.	0.88	b.	1.40	b.	1.31	b.	1.27
	c.	---	c.	-0.10	c.	+2.91	c.	+3.41
Rio Cojedes (Puente El Baul)	a.	1.76	a.	1.70	a.	2.37	a.	3.79
	b.	0.22	b.	0.25	b.	0.66	b.	1.74
	c.	---	c.	-0.06	c.	+0.67	c.	+1.42
Rio Tucupido (Puente Tucupido)	a.	0.91	a.	1.53	a.	2.08	a.	4.78
	b.	0.07	b.	0.47	b.	0.19	b.	0.25
	c.	---	c.	+0.62	c.	+0.55	c.	+2.70
Rio Apure (San Fernando)	a.	38.55	a.	38.52	a.	40.02	a.	41.81
	b.	0.24	b.	0.48	b.	1.14	b.	1.60
	c.	---	c.	-0.03	c.	+1.50	c.	+1.79
Rio Arauca (El Yagual)	a.	2.74	a.	3.08	a.	4.76	a.	5.02
	b.	0.60	b.	0.62	b.	0.19	b.	0.30
	c.	---	c.	+0.34	c.	+1.68	c.	+0.26
Rio Capanaparo (Hato Uranon)	a.	1.61	a.	1.41	a.	2.28	a.	4.95
	b.	0.50	b.	0.66	b.	0.71	b.	1.98
	c.	---	c.	-0.20	c.	+0.87	c.	+2.67
Rio Meta Cararabo	a.	3.21	a.	3.73	a.	6.11	a.	7.48
	b.	0.90	b.	1.22	b.	1.15	b.	1.16
	c.	---	c.	+0.52	c.	+2.38	c.	+1.37
Rio Caura Maripa	a.	2.96	a.	2.86	a.	4.42	a.	6.39
	b.	1.22	b.	1.17	b.	1.35	c.	1.10
	c.	---	c.	-0.10	c.	+1.56	c.	+1.97

Table 22. Orinoco crocodile nesting schedules in relation to river flooding regime.

River	Flooding Regime	Egg Hatching Dates
Tucupido	early	late March- early April
Caura	intermediate	late March- early April
Orinoco	intermediate	early- mid April
Capanaparo	late	late April- early May
Cojedes	late	late April- early May

FIGURE 1. Location of 10 major crocodile populations or geograhic locations mentioned in the text.

1. Rio Capanaparo (Apure State)
2. Rio Cinaruco (Apure State)
3. Rio Tucupido (Portúguesa State)
4. Rio Cojedes/Sarare (Cojedes/Portuguesa States)
5. Camatagua Reservoir (Aragua State)
6. Rio Guarico/Cano Rabanal (Guarico State)
7. Rio Manapire (Guarico State)
8. Rio Cuchivero (Bolivar State)
9. Rio Caura (Bolivar State)
10. Rio Ventuari (T.F. Amazonas)

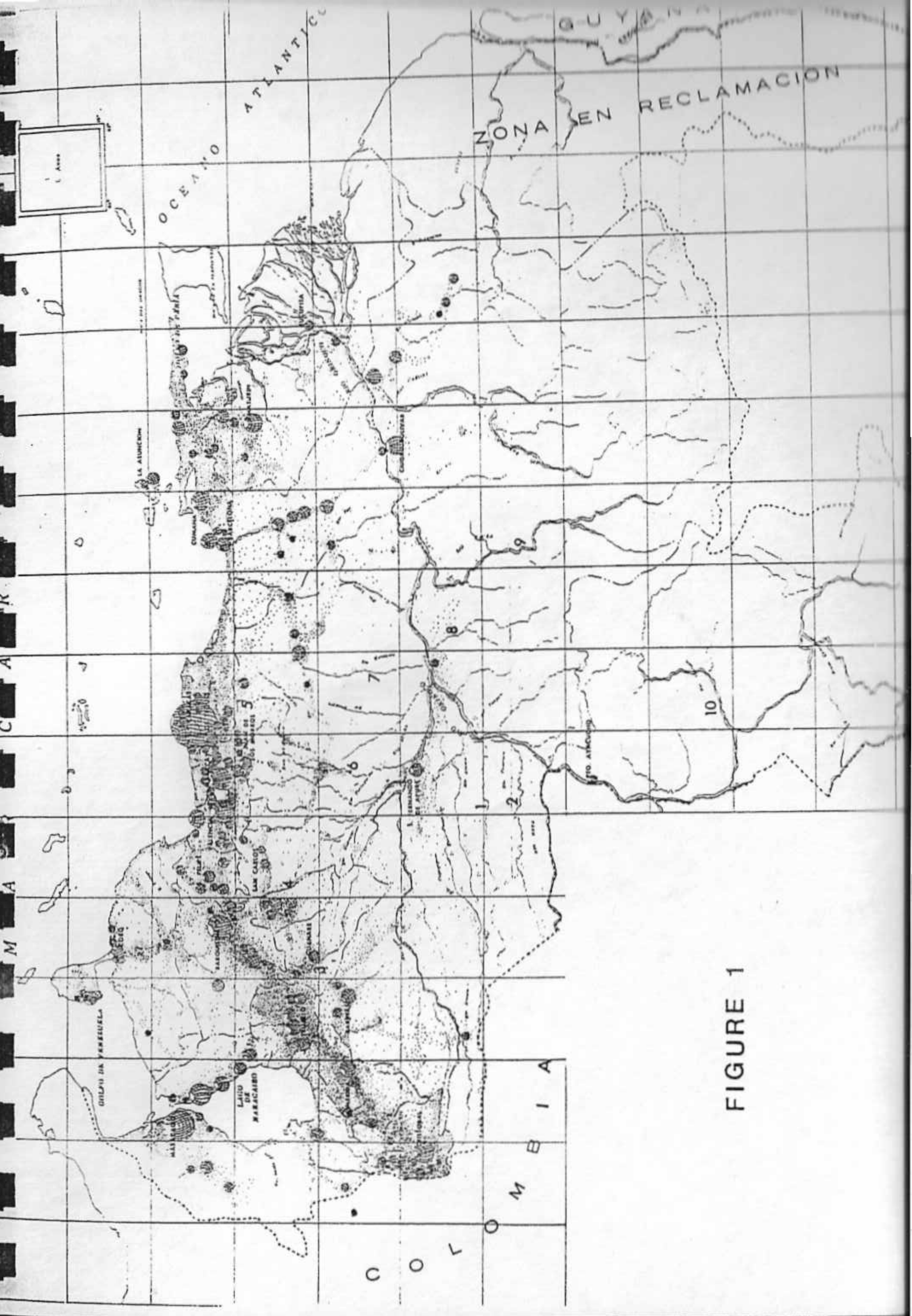

FIGURE 2. Map of the Rio Capanaparo from the confluence of the Rio Riecito downstream to the Rio Orinoco. The 10 river sections defined during the aerial surveys are delimited.

FIGURE 2

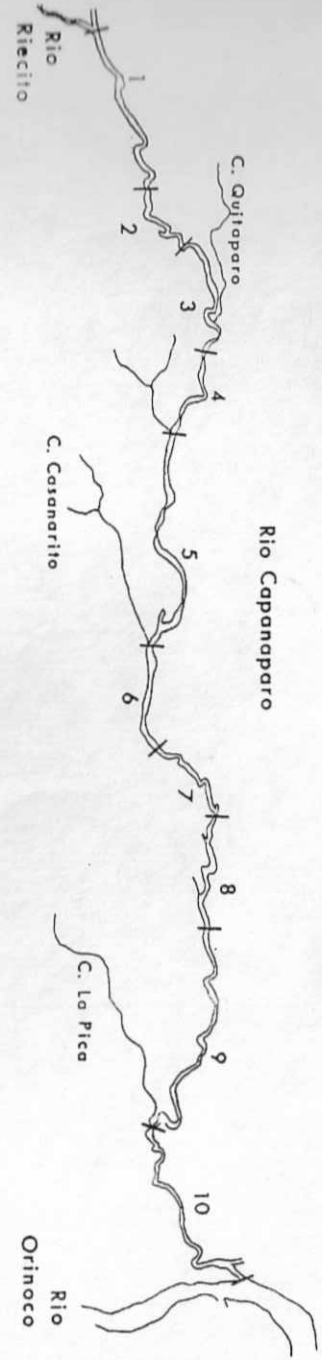

FIGURE 3. Sonagram of male Orinoco crocodile advertisement display. Two headslaps followed by 4 roars, bubbling and a fifth roar. Produced by a 3.7 m male, 10 Feb. 1985 at 0550 hours.

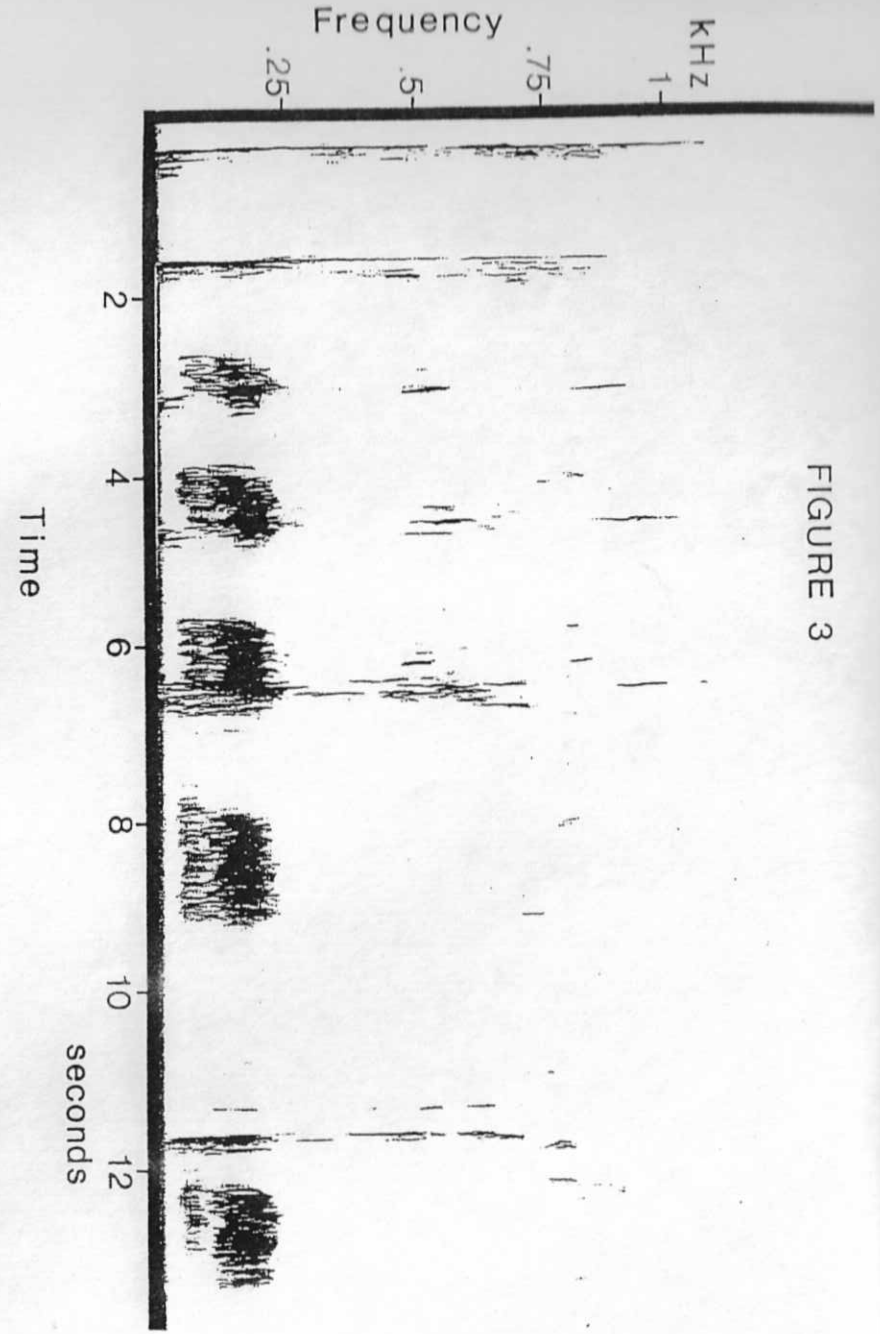

FIGURE 4. Frequency of male advertisement displays by hour of day. Data from two captive males on Hato Masaguaral over a 24 month period 1985–1986.

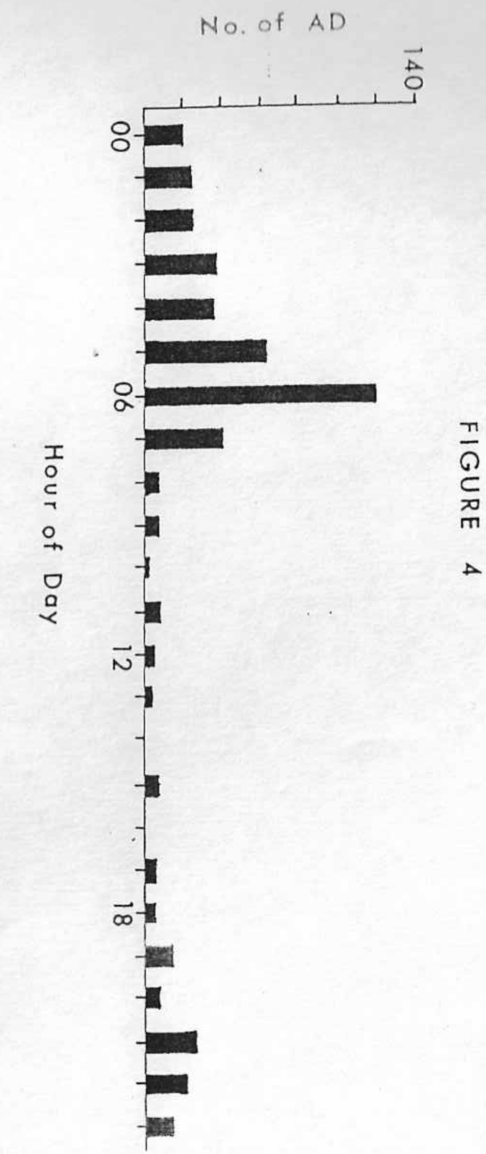

FIGURE 5

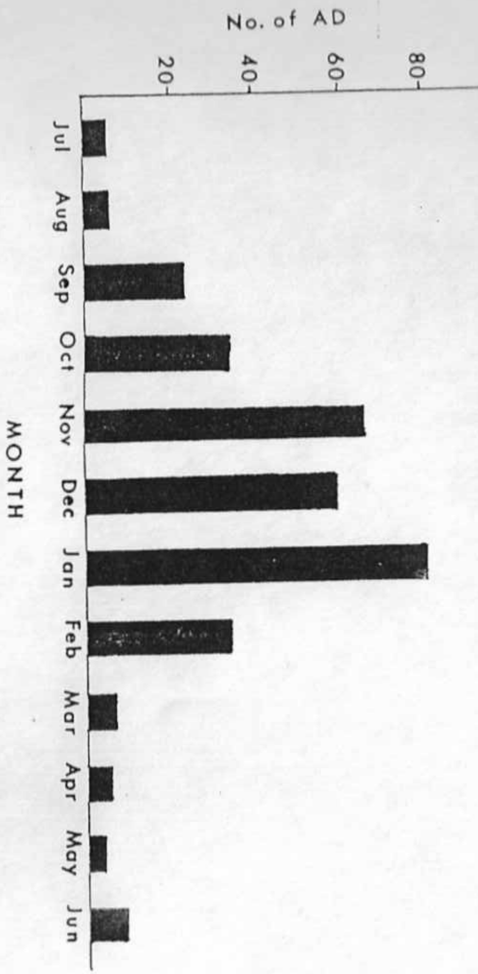

FIGURE 5. Frequeny of male advertisement displays by month of year. AD's from two captive males on Hato Masaguaral 1985-1986.

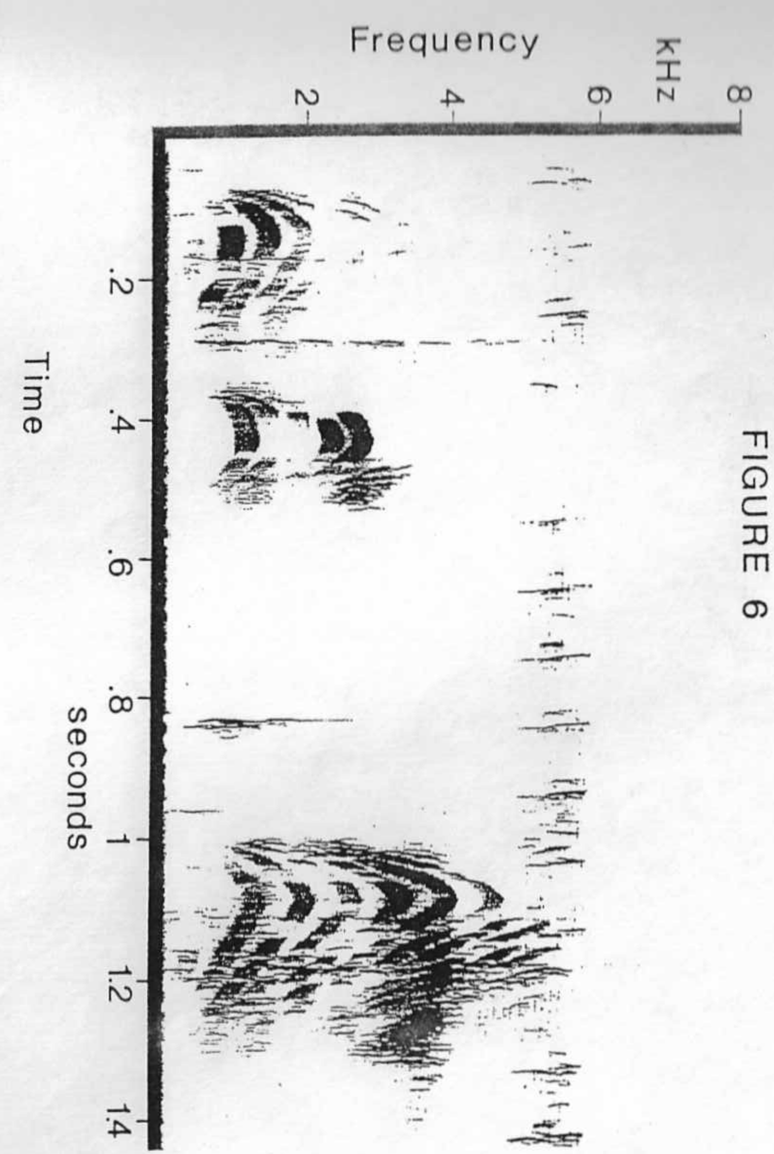

FIGURE 6. Sonagram of an Orinoco crocodile hatchling "distress" call. Produced by 1 month old hatchling on 6 May 1987 at Hato Masaguaral.

APPENDICES

Appendix 1. Godshalk's (1978) list of Venezuelan rivers and reservoirs reported to contain Orinoco crocodiles. Indented rivers indicate they are tributaries of the preceding non-indented river. (States: Apure-Ap, Barinas-Ba, Portuguesa-Po, Cojedes-Co, Guarico-Gu, Aragua-Ar, Monagas-Mo, Bolivar-Bo, Delta Amacuro-Da, Amazonas-Am).

River	State	Information Source>	
		Interview	Sighting
Suripa	Ba	x	
Caparo	Ba	x	
Portuguesa	Po/Co/Gu/Ba	x	
Gauche	Co	x	
Guanare	Po/Ba	x	
Cano Igues	Po/Co	x	
Cojedes	Co/Po	x	x
San Carlos	Co	x	
Tinaco	Co	x	
Chirgua	Co/Gu	x	
Tiznados	Gu	x	
Arauca	Ap	x	
Brazo Guarico	Ap	x	
Cano Guaritico	Ap	x	
San Felipe	Ap	x	
Cunaviche	Ap	x	
Claro	Ap	x	
Meta	Ap	x	x
Cinaruco	Ap	x	x
Cano Juriepe	Ap	x	
Cano Potrerito	Ap	x	
Capanaparo	Ap	x	x
Riecito	Ap	x	
Quitaparo	Ap	x	
Cano El Naure	Ap	x	
Guarico	Gu/Ar	x	
Embalse Guarico	Gu	x	
Embalse Camatagua	Ar	x	
Parguaza	Bo	x	
Suapure	Bo	x	
Ventuari	Am	x	
Caura	Bo	x	
Guanipa	Mo	x	
Orinoco Delta	Da	x	
Orinoco	--	x	

Appendix 2. 1986-87 aerial surveys to census crocodile populations in Venezuela. Records give date of survey, location, starting and ending point and times. Information is also provided on the rivers censused during manatee surveys in 1986 (from O'Shea et al. 1986).

1986 Crocodile Surveys

15 April: Embalse de Guarico, 1638-1731 h
16 April: Rio Caura, mouth to Salto Para, 1033-1215h
17 April: Rio Orinoco, Cuidad Bolivar to Rio Arauca, 0757-1206h
Rio Orinoco, Rio Meta-Capanaparo, 1518-1703 h
18 April: Rio Arauca, Paso Arauca-Elorza, 0809-1042 h
Rio Arauca, Elorza-Mata Azul, 1253-1312 h
Rio Capanaparo, Cano Cubarro-San Pablo, 1322-1618
19 April: Rio Capanaparo, San Pablo-Rio Orinoco, 0908-1028h
Rio Orinoco, Capanaparo-Arauca, 1028-1100h
Rio Cinaruco, Rio Orinoco-Brazo Cinaruco, 1331-1600 h
Rio Tucupido, 31 km downstream to dam, 1752-1815 h
20 April: Rio Tucupido, dam to 31 km upstream, 1338-1403 h
21 April: Rio Manapire, Rio Orinoco to Santa Rita, 1024-1108h
Rio Aguaro, 300 deg Santa Rita to 50 km downstream, 1116-1143 h
Cano Caballo, Paso El Caballo to Hato Rabanal, 1220-1242 h
Embalse de Camatagua, 1458-1600 h

1987 Crocodile Surveys

13 March: Embalse de Guarico, 1545-1621 h
Embalse Rio Verde, 1645-1710 h
30 March: Embalse de Camatagua, 0855-1009 h
31 March: Rio Orinoco, Rio Apure-Rio Arauca, 1650-1710 h
Rio Arauca, Rio Orinoco-9 km upstream, 1713-1720 h
1 April: Rio Capanaparo, Rio Riecito-Quitaparo, 0840-1001 h
14 April: Rio Capanaparo, Rio Riecito-El Betun, 0832-1025 h
Rio Cinaruco, Camp. Mobil-210 km upstream, 1533-1700 h
15 April: Rio Cuchivero, Rio Orinoco-140 km upstream, 1513-1609 h
16 April: Rio Capanaparo, Cano Casanarito-Rio Orinoco, 0831-0954 h
Rio Claro, 360 deg. Hato Uranon-50 km upstream, 1115-1134 h
Rio Riecito, Rio Capanaparo-84 km upstream, 1606-1640h
17 April: Rio Capanaparo, Rio Riecito-Cano La Pica, 0839-1054 h

Appendix 2.—Continued

1986 Manatee Surveys

Rivers censused for crocodiles during manatee surveys, 25 March-4 April 1986.

Middle Orinoco Tributaries:

Apure	Guariquito
Aro	Orinoco
Arauca	Paragua
Canagua	Portuguesa
Capanaparo	Sarare
Caura	Saripa
Cuchivero	Uyare
Guanare	Ventuari

Orinoco Delta Region:

Cano Pedernales	Rio Grande
Cano Macareo	Rio Barima
Cano Mariusa	Rio Amacuro
Cano Araguao	Rio Arature
Cano Yaguarimabo	

Appendix 3. Method of estimating crocodile population size based on calculation of a sighting fraction for aerial survey censuses of the Rio Capanaparo, April 1987.

Comparison of the size-class distribution of crocodiles in river section 3 estimated from 1) aerial surveys and 2) nocturnal spotlight counts (see Table 16), revealed that crocodiles between 1-2 m TL were underrepresented in the aerial census figures. Hence, two sighting fractions need to be calculated: P_{1-2} and $P_{>2}$, for crocodiles 1-2 m TL and crocodiles greater than 2 m TL respectively.

Calculation of $P_{>2}$ was based on the resighting of "individual" crocodiles during aerial surveys. Within each river section, crocodiles greater than 2 meters total length were identified by size-class and location. A resighting was defined as seeing the same sized crocodile (within 1 meter size classes), two kilometers or less from a previous sighting. It was felt that this methodology would overestimate the frequency of resightings, and hence result in a smaller correction factor, and a conservative estimate of population size. If P is the probability of seeing any one crocodile (over 2 m TL) during an aerial survey, then the frequency of resightings should approximate P^2.

Resighting values (p^2) were calculated by dividing the number of resightings by the best estimate of total number of individual crocodiles (>2 m TL) in that river section.. The mean of all values was used as the best estimate of $P_{>2}$.

River Section	Flight Comparison	Total # Ind. Crocodiles	Number of Resightings	P^2	P
1	1-2	4	1	0.25	0.50
	2-3	4	1	0.25	0.50
	1-3	4	C	0.00	0.00
2	1-2	8	2	0.25	0.50
	2-3	8	1	0.13	0.35
3A	1-2	19	2	0.11	0.32
	2-3	19	5	0.26	0.51
	1-3	19	3	0.16	0.40
3B	1-2	7	1	0.14	0.38
4	1-2	5	2	0.40	0.63
5	1-2	5	1	0.20	0.45
6	1-2	4	0	0.00	0.00
	2-3	4	0	0.00	0.00
	1-3	4	0	0.00	0.00
7	1-2	5	0	0.00	0.00
8	1-2	5	0	0.00	0.00
9	1-2	4	0	0.00	0.00
10	---	-	-	----	----
Mean					0.27

Appendix 3.--Continued

Because of the small number of crocodiles less than 2 m TL that were "resighted" (n=1), a different method was used calculate P_{1-2}. A comparison of the size-class distribution data for aerial and nocturnal censuses reveals an apparent 55% decrease in the representation of 1-2 meter animals in the aerial counts. If we assume that the sighting fraction of all crocodiles over 2 meters does not vary with size, this suggests that the sighting fraction for 1-2 meter crocodiles is only 0.45 that of the larger animals. We can then estimate the sighting fraction for 1-2 m crocodiles as: $P_{1-2}=(0.45)(0.27)=0.12$.

Appendix 4. Hydrological and limnological aspects of major Orinoco River tributaries in Venezuela. Values presented are means with minimum and maximum values in parentheses. All data are from MOP (1972) except Rio Caroni (Alvarez et al. 1986). Hydrological data from 1970, limnological data 1968-1970.

River	Orinoco (Musinacio)	Apure (San Fernando)
River Type	----	Ia
River Flow	33481	2308
(mill. cu. m/sec)	(6609-62999)	(239-5614)
Volume	1055856	72785
(mill. cu. m)		
Turbidity	43	81
(NTU)	(17-87)	(30-195)
Conductivity	37	127
(mohm/cm)	(16-51)	(80-182)
pH	7.3	7.6
	(6.4-8.1)	(7.2-8.0)
Hardness	14	48
(mg/l $CaCO_3$)	(8-22)	(36-70)
Nitrate	0.2	0.3
(mg/l NO_3)	(0.0-0.4)	(0.0-0.8)

River	Arauca (El Yagual)	Capanaparo (Hato Uranon)
River Type	Ia	Ia-b
River Flow	406	---
(mill. cu. m/sec)	(92-728)	---
Volume	12803	---
(mill. cu. m)		
Turbidity	163	10
(NTU)	(90-285)	(0-35)
Conductivity	43	32
(mohm/cm)	(31-63)	(10-62)
pH	7.0	6.8
	(6.8-7.4)	(6.0-7.5)
Hardness	15	10
(mg/l $CaCO_3$)	(12-20)	(2-30)
Nitrate	0.3	0.1
(mg/l NO_3)	(0.0-0.7)	(0.0-0.4)

Appendix 4.--Continued

River	Cinaruco (Camp. Mobil)	Caroni
River Type	Ib	IIa
River Flow	398	---
(mill. cu. m/sec)	(42-1100)	---
Volume	12551	---
(mill. cu. m)		---
Turbidity	3	---
(NTU)	(0-9)	(2.9-14.0)
Conductivity	14	---
(mohm/cm)	(5-63)	(6.2-8.9)
pH	6.3	---
	(5.3-8.2)	(4.7-6.9)
Hardness	3	---
(mg/l CaCO 3)	(0-16)	(2.9-18.0)
Nitrate	0.1	---
(mg/l NO 3)	(0.0-0.9)	---

River	Caura (San Luis)	Suapure (San Pedro)
River Type	IIa-b	IIb
River Flow	3385	214
(mill. cu. m/sec)	(170-8486)	(33-725)
Volume	106749	6748
(mill. cu. m)		
Turbidity	11	
(NTU)	(5-30)	(0-15)
Conductivity	15	16
(mohm/cm)	(7-22)	(7-24)
pH	6.7	6.7
	(6.2-7.3)	(6.0-7.1)
Hardness	7	4
(mg/l CaCO 3)	(4-14)	(2-6)
Nitrate	0.6	0.2
(mg/l NO 3)	(0.0-1.8)	(0.0-1.5)

Note : Hydrological data for Caura are for 1975.

Appendix 5. Habitat and other data collected during nocturnal censuses of habitat usage, Rio Capanaparo, 1987.

CATEGORY	SYMBOLS	SIGNIFICANCE
Species	C	Crocodile; *Crocodylus intermedius*
	B	Baba; *Caiman crocodilus*
	EO	Eyes only
	EO/C	Eyes only, probably a crocodile
Size-class	I	Babas; x<20 cm SVL
	II	Babas; 20<x<60 cm SVL
	III	Babas; 60<x<90 cm SVL
	IV	Babas; x>90 cm SVL
	<0.5	Crocodile; <0.5 m TL
	0.5-1.0	Crocodile; 0.5<x<1.0 m TL
	1.0-1.5	Crocodile; 1.0<x<1.5 m TL
	1.5-2.0	Crocodile; 1.5<x<2.0 m TL
	2.0-2.5	Crocodile; 2.0<x<2.5 m TL
	2.5-3.0	Crocodile; 2.5<x<3.0 m TL
	3.0-3.5	Crocodile; 3.0<x<3.5 m TL
	3.5-4.0	Crocodile; 3.5<x<4.0 m TL
	>4.0	Crocodile; x>4.0 m TL
Distance	<10	Less than 10 m from previous unit (crocodilian)
	10-50	10 to 50 m from previous unit
	>50	More than 50 m from previous unit
Situation	SWOE	Shallow water on edge
	IW-x	In open water, x meters from shore
	OS	On shore
	IVIW	In vegetation in water
	-OFM	On floating mat of vegetation
	-EV	In emergent vegetation
	DT	Among dead trees/shrubs in water

Appendix 5. Habitat and other data collected during nocturnal censuses of habitat usage, Rio Capanaparo. 1987.

CATEGORY	SYMBOLS	SIGNIFICANCE
Species	C	Crocodile; *Crocodylus intermedius*
	B	Baba; *Caiman crocodilus*
	EO	Eyes only
	EO/C	Eyes only, probably a crocodile
Size-class	I	Babas; x<20 cm SVL
	II	Babas; 20<x<60 cm SVL
	III	Babas; 60<x<90 cm SVL
	IV	Babas; x>90 cm SVL
	<0.5	Crocodile; <0.5 m TL
	0.5-1.0	Crocodile; 0.5<x<1.0 m TL
	1.0-1.5	Crocodile; 1.0<x<1.5 m TL
	1.5-2.0	Crocodile; 1.5<x<2.0 m TL
	2.0-2.5	Crocodile; 2.0<x<2.5 m TL
	2.5-3.0	Crocodile; 2.5<x<3.0 m TL
	3.0-3.5	Crocodile; 3.0<x<3.5 m TL
	3.5-4.0	Crocodile; 3.5<x<4.0 m TL
	>4.0	Crocodile; x>4.0 m TL
Distance	<10	Less than 10 m from previous unit (crocodilian)
	10-50	10 to 50 m from previous unit
	>50	More than 50 m from previous unit
Situation	SWOE	Shallow water on edge
	IW-x	In open water, x meters from shore
	OS	On shore
	IVIW	In vegetation in water
	-OFM	On floating mat of vegetation
	-EV	In emergent vegetation
	DT	Among dead trees/shrubs in water

Appendix 5.--Continued

Shore Conformation
(Units 10 meters or less from shore; shore defined as water/land or water/emergent vegetation interface)

Shore gradient:	S	Steep shore bank, approx >30 deg
	M	Moderate grad., approx 10-30 deg
	L	Low grad, approx <10 deg
Vegetation:	WL-	Open shore, land/water interface
	B	Shore mostly bare of vegetation
	S	Low herbaceous or shrubby veg.
	F	Fringing forest
	OT	Overhanging trees
	VL-	Emergent vegetation extends into water
	H	Emergent herbaceous vegetation
	W	Emergent live woody vegetation
	DT	Emergent dead woody vegetation
Soil:	S	Sandy soil
	R	Rocks/pebbles
	O	Organic soil
Wave Exposure	0	No wave action
	1	Ripples, <2 cm amplitude
	2	Small waves, 2-10 cm amplitude
	3	Waves, >10 cm amplitude
Posture	H	Head only, normal posture
	HE	Head elevated, water at jaws
	HL	Head low, eyes, tip of nostrils
	HA	Head alert
	B	Unit floating, back visible
	T	Unit floating, tail visible
	TA	Tail arched