Differential Harvest of American Alligators on Private Lands in Coastal South Carolina

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ABSTRACT: American alligator (*Alligator mississippiensis*) populations in South Carolina recovered following season closure in 1964 and subsequent state and federal protection during the 1970s. A program permitting a limited harvest of alligators on private lands in 7 coastal counties was established in 1995. Following night-light surveys and habitat evaluations, participating landowners were issued a quota by 61-cm size classes for alligators $\geq 122$ cm. The objective of the differential-harvest approach was to harvest alligator size classes in proportion to their occurrence. Approximately 45, 34, 14, and 7 percent of the tags were issued for the four size classes, respectively, during 1995-2001. Overall annual success ranged from 42-80 percent. The 244-cm size class exhibited the highest average success (80 percent) whereas success was lowest (45 percent) in the 122-cm size class. Average total length (TL) was 216 cm (range = 207-225 cm). Annual sex ratio averaged 70.3 percent male (range = 60-75.6 percent). Despite the reluctance of trappers to harvest small alligators, the differential-harvest approach is a tool wildlife biologists can use to prevent the over-harvest of adult alligator size classes.

INTRODUCTION

Alligators have been harvested for over two centuries in the Southeastern United States. For the most part, the exploitation of these animals has occurred with little regard to age, sex or size of harvested animals. More recently, certain cohorts of alligators have been protected from harvest by use of regulations, primarily minimum sizes and harvest techniques, but little work has investigated within-size class harvest rates.

Crocodilians exhibit very complex behavior and social patterns (Lang, 1987), despite their lethargic and solitary appearance. Social organization favors breeding by larger animals of both sexes, which results in a higher and more successful reproductive output. Lang (1987) stated that the harvest of large crocodilians destabilizes long-term social relations, and if continued over a long enough period, reproductive success could decline.

Various studies have determined that adult alligators exhibit sex-specific habitat requirements (Joanen and McNease, 1970, 1972; Rootes and Chabreck, 1993). As such, harvest regulations in several states were designed to minimize harvest of adult female alligators, a mindset that theoretically protects the major breeding segment of populations. Under this harvest approach and effective law enforcement, alligator populations have flourished across their range since legal harvest was reinstated in the early 1970s.

Despite the success of alligator programs across the Southeast, the current harvest approaches have been questioned. Taylor and Neal (1984), Taylor et al. (1991), and Kinler and Taylor (1992) demonstrated that alligator populations could withstand a higher harvest rate. By increasing tag allotments, they found that by default trappers increased harvest of smaller size classes. Nichols et al. (1976) suggested a more direct approach, called proportional harvest rate, where animals are harvested in proportion to their occurrence. Lang (1987) recommended the same strategy, stating it would result in minimal disruption to the existing social order of a population.

Alligators were harvested with essentially no regulations in South Carolina until the season was closed in 1964. Disposal of an occasional nuisance alligator was the only legal harvest that took place over the next 20 years. South Carolina’s alligator population continued to expand as did coastal development, resulting in a formal nuisance alligator program in 1987.

Rural landowners were also burdened with an increased alligator population. Most sought relief under the nuisance alligator program, and attempted to illegally reduce alligator populations. Recognizing the problem, the South Carolina Department of Natural Resources (SCDNR) began development of a private lands alligator...
program in 1991. State harvest programs in Florida, Louisiana and Texas were reviewed. A common recommendation was to implement a proportional harvest approach if possible. Regulations were drafted and approved, and South Carolina’s first alligator season in 31 years was implemented in 1995. The objective of this paper is to provide an overview of the season from 1995-2001, with particular emphasis on the proportional harvest approach.

**STUDY AREA**

There are roughly 204,142 ha of coastal wetlands in South Carolina, of which approximately 14 percent (70,541 ha) are impounded (Tiner 1976). Historically, impoundments were used for the production of tidewater rice (Doar 1936), whereas, presently they serve as waterfowl hunting areas (Strange 1987). The majority of the alligator population in South Carolina is associated with intact wetland impoundments (Wilkinson and Rhodes 1992). Impoundments are primarily brackish and support the highest densities of alligators in South Carolina (Rhodes, unpubl. data).

The open area for the South Carolina private lands season targeted abundant alligator populations in these coastal habitats (Fig. 1). All or a portion of Beaufort, Berkeley, Charleston, Colleton, Dorchester, Georgetown, and Jasper counties were open for harvest. Locations further inland were not included in the harvest area because of difficulties with surveying alligator populations in these habitat types.

**METHODS**

Various media outlets announced the opening of the season in the spring of 1995, and subsequent springs. Landowners submitted an application, which included a map and aerial photograph, to enroll in the program. Biologists reviewed the property during the summer, and conducted a night-light survey if needed. Night-light surveys had already been conducted for several years on representative properties in anticipation of the alligator season opening.

Landowners were mailed a tag quota in late August. The quota included total number of alligators ≥ 122 cm, by 61-cm size class, which could be harvested on the property. To achieve a 15-percent harvest rate, night-light surveys indicated that impoundment alligator populations could sustain a harvest of 1 tag per approximately 50 acres of habitat. Further, estimated 61-cm size class proportions for alligators ≥122 cm from night-light surveys were 50, 30, 15, and 5 percent. Property tag quotas were distributed among size classes by these proportions. Rounding of acreage or number of tags within a size class caused proportions to be shifted slightly on some properties.

Landowners were mailed tags in early September. The four-week season was held from mid September to mid October, and usually included five weekends. Trappers were permitted to harvest alligators from sunrise to 11:00 p.m. by live-capture methods only, such as baited trip snares or snagging. Legal-sized alligators could be dispatched with a firearm no larger than a .22 caliber. A non-CITES tag was placed in the tip of the tail of harvested alligators. Alligator skins were measured and validated after the season, and the harvest tag was replaced with a CITES tag.

**RESULTS**

An average of 16 properties participated in the private lands season from 1995-2001. Annual statewide quotas ranged from 159-395 tags (Fig. 2). Annual statewide harvest was 90-211 alligators. Overall annual success ranged from 42-80 percent, and averaged 59 percent. Average total length (TL) was 216 cm (range = 207-225 cm). Annual sex ratio averaged 70.3 percent male (range = 60-75.6 percent).
Approximately 45, 34, 14, and 7 percent of the tags were issued for the four size classes, respectively, during 1995-2001. Percent of total harvest among the four size classes was 34, 40, 19, and 7, respectively, from 1995-2001 (Table 1). Trappers had the highest average success (80 percent) in the 244-cm size class, whereas success was lowest (45 percent) in the 122-cm size class (Table 2).

**Table 1.** Percent of total alligator harvest among four size classes under a differential-harvest approach, South Carolina, 1995-2001.

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<tbody>
<tr>
<td>122/153cm</td>
<td>39.4</td>
<td>37.5</td>
<td>29.4</td>
<td>34.3</td>
<td>32.2</td>
<td>37.2</td>
<td>30.9</td>
<td>34.4</td>
</tr>
<tr>
<td>183/213cm</td>
<td>42.5</td>
<td>41.4</td>
<td>44.5</td>
<td>40.0</td>
<td>36.7</td>
<td>34.7</td>
<td>38.1</td>
<td>39.7</td>
</tr>
<tr>
<td>244/274cm</td>
<td>12.6</td>
<td>14.8</td>
<td>22.3</td>
<td>17.1</td>
<td>24.4</td>
<td>21.5</td>
<td>21.6</td>
<td>19.2</td>
</tr>
<tr>
<td>305cm+</td>
<td>5.5</td>
<td>6.3</td>
<td>3.8</td>
<td>8.6</td>
<td>6.7</td>
<td>6.6</td>
<td>9.3</td>
<td>6.7</td>
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**Table 2.** Percent of alligator tag quotas filled among four size classes under a differential-harvest approach, South Carolina, 1995-2001.

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<tr>
<td>122/153cm</td>
<td>64.1</td>
<td>60.0</td>
<td>33.9</td>
<td>43.9</td>
<td>31.5</td>
<td>48.4</td>
<td>31.6</td>
<td>44.8</td>
</tr>
<tr>
<td>183/213cm</td>
<td>98.2</td>
<td>93.0</td>
<td>69.6</td>
<td>68.9</td>
<td>46.5</td>
<td>56.8</td>
<td>50.5</td>
<td>69.1</td>
</tr>
<tr>
<td>244/274cm</td>
<td>100.0</td>
<td>100.0</td>
<td>83.9</td>
<td>66.7</td>
<td>62.9</td>
<td>81.2</td>
<td>65.6</td>
<td>80.0</td>
</tr>
<tr>
<td>305cm+</td>
<td>70.0</td>
<td>72.7</td>
<td>38.1</td>
<td>69.2</td>
<td>33.3</td>
<td>53.3</td>
<td>52.9</td>
<td>55.6</td>
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**DISCUSSION**

Using a differential-harvest approach, also called proportional harvest, is not a new concept but it is rarely used. Nichols et al. (1976) demonstrated that adult alligator in Louisiana were exploited at a higher rate than their occurrence in the population and was the first to suggest proportional harvest. Taylor and Neal (1984), Taylor et al. (1991), and Kinler and Taylor (1992) verified that alligator populations could withstand an overall higher harvest rate if the 122- and 153-cm size classes were more heavily exploited.

South Carolina was the first state to implement it on a statewide basis. Louisiana indirectly investigated the concept on several occasions (Taylor and Neal, 1984; Taylor et al., 1991; Kinler and Taylor, 1992) before employing “bonus tags” statewide in 1999 in an attempt to harvest additional alligators less than 183 cm.
Overall success (defined as percentage of tags filled) in South Carolina was lower than success rates reported elsewhere. Success in South Carolina averaged 59 percent under the differential-harvest approach. Success rates in Louisiana without a differential harvest have annually averaged over 90 percent since 1973, and have consistently been above 95 percent since the mid 1980s (Kinler, 2002). Woodward et al. (1992) reported an 84 percent success rate for three lakes in Florida without differential harvest from 1981-90.

The lower success rate observed in South Carolina under differential harvest results not from the lack of alligators but trapper habits. Harvesting alligators is a strong tradition in Louisiana and Florida whereas it was historically only practiced by a small core of people in South Carolina. Most of the applicants in South Carolina’s private lands season participate for recreation and novelty rather than as a commercial means. Although the 122-cm size class had the lowest success rate (45 percent), other size classes were also substantially under-utilized, particularly the 305-cm-plus size class that had only a 56 percent success rate. Based on these success rates, it is theorize recreational trappers have a stigma against harvesting small alligators. Louisiana trappers utilized over 90 percent of bonus tags issued (Kinler, 2002), which is expected where a more commercial attitude is in place; however, trappers still tended to take the largest animals permitted under the bonus tag program. Additional time demands from other recreational activities probably contributed to the lack of harvest of larger alligators in South Carolina.

Other biological measurements of harvested alligators in South Carolina were similar to harvested populations reported elsewhere. Average TL (216 cm) and sex ratio (70 percent males) in South Carolina was comparable to populations in Florida (Woodward et al., 1991), Louisiana (Kinler, 2002), and Texas (Cooper and Slaughter 2001). Average TL and percent males was lower in South Carolina when more alligators < 183 cm were harvested, which would be expected when harvest is directed towards smaller size classes. Although a differential-harvest approach is in place in South Carolina, the current rate of effort appears to mimic alligator populations not under differential harvest, which is probably under-utilizing the alligator resource in South Carolina.

The best measure to determine if a differential-harvest approach is fully utilizing the alligator resource would be size-class distribution of harvested animals versus population size distribution. Approximately 45, 34, 14, and 7 percent of the tags were issued for the four size classes, respectively, during 1995-2001 in South Carolina. This was based on size classes observed during night-light surveys during pre-harvest years. The average size-class distribution of harvested alligators was 34, 40, 19, and 7 percent, for the four size classes, respectively. This indicates that harvest in South Carolina was still skewed towards larger alligators but the largest size class was not over-exploited, which is a goal of the differential-harvest approach.

The distribution of the 2001 harvest for the same four size classes in Louisiana was 11, 62, 21, and 6 percent (Kinler, 2002). This contrasts to the South Carolina harvest, especially for the first two size classes. Even when bonus tags are figured in the statewide harvest, the <183-cm size class only approaches 15 percent and could probably be even higher without impacting populations (Kinler, pers. comm.).

Woodward et al. (1992) also found harvest of alligators in Florida were skewed towards larger alligators. For Lochloosa, Newnams and Orange lakes, harvest distribution over the four size classes was 45, 27, 15, and 13 percent from 1981-90, which contrasts to both Louisiana and South Carolina data. They reported the proportion of bull alligators harvested decreased with time relative to smaller alligators (< 274 cm), but it varied by area. They concluded this could have been related more to wariness of large alligators rather than an actual decline. Further, they stated that size distributions of harvests conformed relatively well night-light survey distributions on two of the three lakes.

Whether under a non-differential- or differential-harvest approach, alligator populations in all three states are reported to be stable or increasing. Alligator biologists have felt that the <183-cm size classes were the most exploitable cohorts, however, this logic could include animals less than 244 cm. These data indicate that alligator populations may be able to sustain a harvest favoring the larger size classes, no matter what harvest approach is implemented, as long as the population harvest rate is biologically acceptable (i.e. 15 percent or less) and the total harvest distribution for alligators >244 cm does not exceed approximately 25 percent.

Woodward et al. (1992) stated proportional harvests with respect to size classes are disproportionate with respects to levels of growth rates, and therefore, result in under-harvest of smaller, faster growing alligators relative to larger, slower growing individuals. They suggested that harvests might be sustainable by progressively weighting the harvest toward smaller alligators. An alligator growth study in South Carolina by
Wilkinson and Rhodes (1997) showed disproportionate growth rates by size classes. If harvest pressure in South Carolina increases in the future an adjustment of harvest rates for larger size classes might be needed to further conserve large, adult alligators.

Alligator trappers will always want to harvest the most and largest alligators possible. In many cases, harvest methods condition large animals to be wary (e.g. light shy) and avoid harvest. Reduced disturbance, habitat types, and other harvest methods, usually involving bait, may not instill the same level of wariness. Therefore, large alligators might be over-exploited. This is potentially the situation in South Carolina. Given these conditions, utilizing a differential-harvest approach that applies a 15-percent harvest rate by 61-cm size classes for alligators \( \geq 122 \) cm under appears to produce a sustainable supply of large alligators for trappers and wildlife viewers alike.

LITERATURE CITED


The Current Status and Conservation of Chinese Alligator
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ABSTRACT: Chinese alligator is an endemic species in China and has been listed as category one species under the key state protected wildlife. It is also considered as the most endangered species of 23 crocodiles in the world by IUCN. Since 1980s, the Chinese Government has launched a serial conservation measures and scientific researches. So far, the captive population has reached over 10,000 individuals with annual increasing rate of 2,000 individuals. However, with land exploitation change, illegal hunting, environmental pollution and natural disasters, the wild population is challenging the threats of extinction. The recent survey shows that the current wild population is less than 200 individuals and decreasing at the annual rate of 4-6%. To save China ancestor dragon, with supports of international organizations and interested individuals, State Forestry Administration of China commenced on some conservation projects including habitat restoration, ranching, captive breeding and reintroduction. This paper presents the detailed progresses of China for saving Chinese Alligator within recent two years and the active actions behind two international workshops in Heifei and Guangzhou, 2001.

1 CURRENT POPULATION STATUS

1.1 Wild Population Decreasing

According to historical records, until the middle of 20th century, Chinese alligators could be found along the middle and lower reaches of Yangtze and Shaoxing river basins. The evidence shows this species was abundant and widely distributed from Shanghai on the lower reach of Yangtze River up to Jiangling County of Hubei Province. 300-500 (Chen, B. H, et al, 1981) individuals were recorded in the early of 1980s. With land reclamation, illegal poaching, environmental pollution and natural disasters, the wild population is decreasing rapidly. So far, the wild population is only restricted to small, narrow and isolated plots which belong to Jinxian county, Guangde county, Nanglin county, Xuanzhou district, Ningguo city, Maanshan city and Dangtu county of the southern Anhui Province, as well as Changxing county of Zhejiang Province. It was also reported that the species was found in Yixing County of Jiangsu Provinces (no record in the recent survey). Thorbjarnarson (2000) reported that the wild population is less than 200 individuals with annual decreasing rate of 4-6%. The largest population size in one site only consists of 10-11 individuals (total 4 sites) and usually only one of them is female. Most colonies consist of 2-5 individuals.

1.2 Captive population increasing

With the success of the captive breeding techniques in 1982, the captive population reached over 10,000 individuals till the end of 2001. Among them, about 10,000 individuals in Anhui Breeding and Research Center for Chinese Alligator (ABRCCA) and 366 individuals in Yingjiabian Nature Reserve of Zhejiang Province. The annual increasing rate of ABRCCR is about 1500-2000 individuals. So far, the second filial generation of captive bred Chinese alligator of ABRCCR can be successfully bred. In addition, there are more than 100 Chinese alligators in zoos around China.

2 CURRENT CONSERVATION STATUS

2.1 Legal supports

In 1972, the Chinese Alligator was listed as the state protected species. In 1988, Wildlife Protection Law of People’s Republic of China was issued and brought into implementation. Meanwhile, the State Council also formulated the list of category one and two species under the key state protected wildlife. The Chinese Alligator
was listed as category one species. After then, related regulations and rules were also issued at national, provincial and local levels.

2.2 Establishment of Nature Reserves

Anhui Chinese Alligator Nature Reserve covering a total area of 43,300 hm$^2$ was established by provincial government in 1982 and promoted as national nature reserve by State Council in 1986. The reserve includes 13 protection and management stations covering 41 hm$^2$ distributed in five counties, which is co-managed by Anhui Breeding and Research Center for Chinese Alligator.

The resident of Changxing County of Zhejiang Province spontaneously fenced the habitat for the remained wild Chinese alligators. In 1988, Department of Forestry of Zhejiang Province confirmed it as a provincial nature reserve, which covers 120 hm$^2$ with core area of 3 hm$^2$.

2.3 Establishment of captive breeding centers

To prevent the Chinese Alligator from field extinction, Department of Forestry of Anhui Province established Anhui Breeding and Research Center for Chinese Alligator in 1979. The Center collected 212 wild individuals from random distribution sites for captive breeding. With continued efforts of experts from Anhui Normal University and the staff of ABRCCR, a set of captive breeding technique was developed in 1982. Meanwhile, 147 hatchlings were successfully hatched out in this year. The second filial generation was successfully born in 1987. From that time, the number of the captive-bred alligators has been increased continuously. At present, the rate of hatching, surviving and preserving are 90.5%, 97.9% and 85% respectively. The research has reached international level and awarded the Second Class Prize for Science and Technology Development by State Forestry Administration (SFA) (former Ministry of Forestry) of China.

Zhejiang Changxing Breeding Center for Chinese Alligator was founded in 1979. The first filial generation was hatched out in 1984 and the second filial generation was born successfully in 1997.

2.4 Public Education

Since the end of 1970s, the Chinese government has commenced on public education on wildlife conservation, especially to students. With the formulation of Wildlife Protection Law, governmental departments at national, provincial and local level initiated Wildlife Conservation Month all over the country. To improve the conservation awareness and good understanding of the Chinese Alligator, the local departments have conducted serial activities such as poster setting, legal popularization, media exposure, workshop, materials distribution, eco-tourism and so on.

2.5 Scientific Researches

Some scientific researches on the Chinese Alligator have been launched since the end of 1970s. So far, the main research fields include population counting, distribution, burrow selection, home range, captive breeding, physiology, morphology and conservation genetics etc. The results provide scientific basis for the upcoming projects of Chinese Alligator protection.

2.6 Commerce Management

In 1992, the 8th meeting of Parties of CITES approved the commercial utilization of the individuals of second filial generation of captive bred Chinese Alligator. SFA of China has strictly taken measures to efficiently manage its commercial activities including strict control of the number of individuals for commercial purposes, strict limitation of the number of units of utilization and trade, and fund raising from the commercial activities by the utilization to the conservation and captive breeding of Chinese Alligator.
2.7 International Cooperation

International cooperation played an effective role in development of Chinese Alligator protection. The Chinese Government always keeps a positive attitude to the international cooperation concerning Chinese Alligator protection.

By the end of 1970s, the experts of China and U.S.A. jointly conducted a cooperative survey on Chinese alligators, which preliminarily recognized the population size and distribution of the Chinese Alligator. Since the end of last century, with the supports of WCS, we have conducted some researches on biological conservation. In 2001, with the supports of some international organizations including CSG, WCS, WWF and Australia-China Council, SFA sponsored two international workshops in Anhui and Guangzhou concerning re-introduction of Chinese alligators and commerce management in crocodiles.

3 MAIN ACHIEVEMENTS WITHIN RECENT TWO YEARS

Since the approval and release of ‘China Action Plan for Conservation and Re-introduction of Chinese Alligator’ and ‘Guangzhou Advocation on Coordination Between Crocodile Protection and Industry Development’, which were separately developed in Hefei and Guangzhou International workshops in 2001, SFA has strictly implemented the proposed activities step by step and made a great of progress on saving Chinese Alligator project. The specific activities were completed as followings.

3.1 Developing two conservation planning documents

With scientific and technical supports from some relevant institutes/universities/colleges, two plan documents including Construction Plan of Saving Chinese Alligator and Construction Plan of Chinese Alligator Breeding Base have been developed at the end of 2001, which are guideline document for saving Chinese Alligator project. With rationale of efficiency, innovation and cost, the Chinese government is planning to launch related activities in Anhui, Jiangsu and Zhejiang Provinces step by step.

3.2 Habitat restoration project

So far, we have negotiated with the local governments on the land-use within 6 proposed re-introduction sites of Anhui Province and got approved. One of the proposed sites, Gaojingmiao Forestry Farm (a state-owned forestry farm) is in the process of habitat restoration. The captive alligators will be re-introduced according to the original plan.

3.3 Re-introduction project

In the ABRCCA, some wildness ponds have been established and some re-introduced alligators will be released for semi-wildness before the implementation of the full project. So far, a total of 1.8 million US$ has been invested to improve the infrastructures and instruments of ABRCCA, most of investment come from the central governmental finance.

Another reintroduction site in Zhejiang Province is Taohuagou at Changxing County, covering 467 hm², which is also a state-owned forestry farm. The local forestry department with the support of the central government initiated the re-introduction project at this place. A total of 1.45 million US$ has been invested to establish a captive breeding base.

3.4 Habitat evaluation project

At the beginning of this year, with the financial support of SFA, Habitat Quantization Evaluation of Chinese Alligator is undertaken by National Research and Development Center of Wild Fauna and Flora, and cooperated by Anhui Normal University. The project aims to recognize the wild population size and distribution, surveys and evaluates wild habitat, probes habitat selection pattern, determines suitable habitat standard, and put forward protection and management strategy. The final results will provide reasonable basis for the reintroduction site selection and habitat management.
3.5 The proceeding of two international workshops


3.6 Establishment of volunteer group for technical supports and consultants

In response to the advocacy of two international workshops, SFA has appointed Mr. Jiang Hongxing as contactor of this volunteer group and national coordinator, whose correspondence address is: National Research and Development Center of Wild Fauna and Flora, P.O Box 1928, PC: 100091, Beijing, P.R. of CHINA. For further information, please browse the website: www.wildlife-plant.gov.cn

4 NEXT URGENT ACTION PLAN

To efficiently promote implementation of saving Chinese Alligator project and rehabilitate its wild population, some pilot actions have been identified and will be put into practice step by step by State Forestry Administration of China consulted with experts at home and abroad.

4.1 Seek related technical supports for saving Chinese Alligator project

Effective technical supports are the foundation for the success of project implementation. Considering the current situation, key techniques include monitoring technique for the current wild population, ranching population, wildness population; wildness technique, especially on raising foraging capacity of captive alligators; conservation and management technique; and commercial utilization and management technique for the captive Chinese Alligator and other introduced crocodiles.

4.2 Launch pilot scientific researches

The results of scientific researches provide reasonable basis for conservation and management business. It is imperative to initiate habitat evaluation and conservation genetics projects to guide identification of suitable re-introduction sites and released population structure. Meanwhile, monitoring for the current wild population and released alligators including behavior, viability, habitat selection and activity range, also should be done to review the project progress.

4.3 Conduct training and field tour

With regards to the related techniques, SFA prepare to dispatch one or two delegation to visit some overseas famous farms, ranching farms, nature reserves and colleges/institutes to learn advanced techniques and experience in 2003. Meanwhile, domestic training should also be enhanced.

4.4 Enhance capability building for the breeding bases and nature reserves

To address the needs of re-introduction project and saving enough genetic resources, some related departments have been developed construction plan and approved by the authority. The current infrastructures and instruments will be further improved by the implementation of the project.

4.5 Develop community co-management model

Saving Chinese Alligator project needs concert efforts and contributions from local communities, international society and Chinese governmental departments. How to coordinate and mitigate human-alligator conflicts is a key factor to the success of the project. A reasonable community participatory model will be established with consultation of some experts and stakeholders, as well as public awareness increasing.
4.6 Widen the channels of international cooperation

International cooperation promotes international society recognize China protection business, and China catch up with international progress as well. The Chinese government will continue to enhance international cooperation. The main activities include: to strength information exchange with relevant international organization; to cooperate to run staff training courses; to promote favorable cooperation mechanisms and implement multi-formal cooperation; and to introduce advanced scientific and technical measures, and management experiences.

EPILOGUE

We appreciate all of your continuous supports of finance and technique, and concerns on the Chinese Alligator. We believe, with the close attention and cooperation from related international organizations and colleague, the Chinese Alligator will get rid of the edge of extinction beyond all doubt, and the crocodiles in the world will have a prospective future, and China will contribute greatly to the wildlife conservation and sustainable utilization.

REFERENCES
**Crocodile Conservation at Work in Vietnam; Re-Establishing *Crocodylus siamensis* in Cat Tien National Park**

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**ABSTRACT:** The Siamese Crocodile *Crocodylus siamensis* is classified by IUCN as globally critically endangered. Up to two decades ago, the species was abundant in a wetland ecosystem currently located in Cat Tien National Park – southern Vietnam. Hunting for meat and to stock crocodile breeding farms decimated the population and the species was regarded to be extinct from the Park. This paper presents the activities undertaken to re-establish the species in Cat Tien National Park over the last two years. Crocodiles, donated by a private farmer in Ho Chi Minh City, have been DNA tested to avoid the release of mixed breed individuals (*C. siamensis* x *C. porosus* and *C. rhombifer*). From December 2001 onward, nineteen crocodiles have been released in the Park. Initial monitoring data suggests a stable population has been established. The programme is scheduled to continue over the next two years.

**INTRODUCTION**

Cat Tien National Park is located about 150 km North of Ho Chi Minh City, on the plains of the Dong Nai River, South of Vietnam’s Central Highlands. It is situated in Dong Nai, Lam Dong and Binh Phuoc Provinces but management is in the hands of the central Government’s Ministry of Agriculture and Rural Development). The Park measures about 75,000 ha but is divided in two separated sectors; Cat Loc in the North and Nam Cat Tien in the South (see Map 1). Since 1998, the Park receives substantial financial and technical support from The Netherlands Government through the WWF - Cat Tien National Park Conservation Project.

Cat Tien National Park is located in the monsoon tropical region with a distinct wet and dry season. The topography is characterised by areas with steep hills and flat areas. Although altitudes range only from 200 to 600 metres above sea level, slopes are relatively steep. The Dong Nai River borders the Nam Cat Tien sector in the East and the Cat Loc sector in the West and North. The northern central section of Nam Cat Tien is poorly drained and contains an area of small streams, lakes and seasonally inundated grasslands (Cox et al., 1995).

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**Map 1.** Cat Tien National Park
The Park harbours the last remaining sizeable lowland rainforest in southern Vietnam which consists of a wide variety of habitats. These include:

- primary and re-growth evergreen tropical lowland rainforests dominated by Dipterocarpaceae,
- primary and re-growth semi-evergreen tropical lowland rainforests dominated by *Lagerstroemia* spp.,
- freshwater wetlands with open lakes and seasonal floodplains containing *Saccharum spontaneum*, *S. arundinaceum* and *Neyraudia arundinacea*,
- flooded forests dominated by *Hydnocarpus anethminicata* mixed with *Ficus benjaminica*, and
- areas severely denuded by warfare dominated by bamboo and open grasslands.

The Park hosts a rich variety of wildlife. A total of 99 mammal, 311 bird, 69 reptile and 30 amphibian species have been confirmed to occur in the Park. These include rare and endangered species such as Javan Rhinoceros *Rhinoceros sondaicus annamiticus*, Asian Elephant *Elephas maximus* and Gaur *Bos gaurus* and nine primate species, albeit all in rather low numbers (Polet et al., 1999; CTNP, 2000). Orange-necked Partridge *Aborophila davidi* is endemic to the Park area (Atkins and Tentij, 1998).

**SIAMESE CROCODILES IN CAT TIEN NATIONAL PARK**

Cat Tien National Park hosted large numbers of Siamese Crocodile *Crocodylus siamensis* in earlier times. They occurred on the Dong Nai River but high concentrations could be found in the wetland complex in the northern section of Nam Cat Tien (see Map 2). One of the lakes in this complex is called Bau Sau (Crocodile Lake). The Bau Sau wetland complex has a wet-season maximum circumference of about 2,670 ha and a minimum dry-season circumference of about 150 ha (Wuytack, 2000). Large areas of the Bau Sau wetland habitat are intact and currently well protected.

Ho Thu Cuc (1994) reported that wild populations of Siamese crocodile in Vietnam were restricted to Suoi Trai Nature Reserve in Khanh Hoa Province, Lac Lake in Dak Lak Province and Nam Cat Tien National Park and that no more than 100 individuals survived in the wild in Vietnam. A crocodile was caught in the Dong Nai River in 1989 when fishermen were using explosives. In the same year a small crocodile was observed by Cat Tien National Park staff in the Dong Nai River near the Park’s headquarters. Villagers from Dak Lua village reported to have last seen an 80 kg crocodile in 1996 and in the same year they caught a 50 kg crocodile in the Bau Sau wetland complex (Bembrick and Cannon, 1999). In 1994 a Russian scientist claims to have seen a crocodile in a small pond inside the forest (Andrei Kouzenetsov, pers. comm.). Cat Tien National Park staff have not observed crocodiles since 1996 and it has been concluded that there are no Siamese crocodiles remaining in Cat Tien National Park although there is a possibility of a few animals surviving in areas which are difficult to access (Bembrick and Cannon, 1999). Platt and Ngo Van Tri (2000) came to the same conclusion after a brief survey in Cat Tien National Park. The Siamese crocodile is now regarded to be one of the most critically endangered crocodiles in the wild in the world although captive populations in breeding farms number many thousands (Ross, 1998).

The decline of the Siamese crocodile in Cat Tien National Park was due to vigorous hunting of adults for their skin and sub-adults sold live to crocodile breeding farms; eggs were never harvested (Bembrick and Cannon, 1999). Since the mid-1970’s, the crocodile population in Cat Tien National Park has dwindled, most dramatically between 1975 and 1985. Hunters came from the Mekong Delta and Dak Lua village; the latter reported to have caught one crocodile per day on average. Hunting took place year-round, but most intensively during the wet season, using baited hooks and lines, nets in the water and rope traps on land (Bembrick and Cannon, 1999). Habitat destruction does not appear to have contributed significantly to the decline of Siamese crocodiles in Cat Tien National Park.

In the 1980’s Cuban crocodiles (*Crocodylus rhombifer*) have been imported into Vietnam. They were distributed between zoos and also ended-up in crocodile farms. Hybridisation between *C. siamensis* and *C. rhombifer* produces larger egg clutches and offspring which seem to grow faster than pure breeds. These features are advantages for the leather industry and most captive crocodiles in southern Vietnam are now hybrids. Hybrid animals remain fertile. Second and third generation off-spring can not be distinguished by eye from pure *C.
siamensis. Therefore, most of the captive crocodile stock available in southern Vietnam is not suitable for a re-establishment programme which requires pure C. siamensis to be released within its historic range.

**Map 2. Crocodile Lake Wetland Complex**

**BACKGROUND TO THE RE-INTRODUCTION PROGRAMME**

The Cat Tien National Park authorities have been seeking to re-establish a Siamese crocodile population since early 1999. Such a move was inspired from a desire to secure an ecosystem which is as complete as possible as an example for future generations.

Under the auspices of the WWF-Cat Tien National Park Conservation Project, a short survey was conducted by Bembrick and Cannon in January 1999 whose main findings have been presented above. Their survey included several visits to crocodile farms in and around Ho Chi Minh City. The owner of one of the farms visited contacted the authorities of Cat Tien National Park later in 1999 and offered to donate a number of crocodiles for release into the Bau Sau wetlands. Based on his breeding records, he was quite certain that the crocodiles he offered were related to crocodiles which were captured live in the same Bau Sau wetlands a few decades earlier and should therefore be pure C. siamensis.

In Vietnam, confiscated wildlife is often released in protected areas. Because there are very few wildlife rehabilitation centres in the country, most wildlife is simply released in a protected area nearest to the confiscation site. It thus happens regularly that species are released outside their natural range. Also, quarantine rules are not observed and thus these releases pose a real threat to indigenous populations of wildlife. Apart from the lack of facilities, most wildlife officials in Vietnam seem to be simply un-aware of issues such as wildlife diseases and introducing non-indigenous species. As a result, many officials tend to believe that re-introducing wildlife is simply a matter of opening a cage or bag.

When the WWF-Cat Tien National Park Conservation Project was invited to support the re-establishment programme, issues such as pure breeds, indigenous species and re-introduction guidelines were discussed at some length. It was agreed that the re-establishment of the Siamese crocodiles would be conducted on the basis of sound science. WWF put forward three requirements for its involvement:

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As hybrids cannot be distinguished from pure animals using external features, all crocodiles should be DNA tested and confirmed to be of pure *Crocodileus siamensis* before being transferred to the Bau Sau area.

The Bau Sau wetland complex has to be strictly patrolled in order to reduce the current high incidence of illegal fishing in the area, where opportunistic fisherman in the area thought to pose a threat to released crocodiles.

A feasibility study should be conducted to assess the suitability of the Bau Sau wetlands as a re-establishment site before release.

The re-establishment programme was conceived and formulated in 1999 by different organisations working together informally. These were:

- Cat Tien National Park as the host and release site of crocodiles.
- A private company crocodile farmer from Ho Chi Minh City who would donate about 20 crocodiles.
- The Saigon Zoo which would provide technical advice and who would be the intermediary with Queensland and Canberra Universities – Australia.
- Queensland and Canberra Universities which would conduct DNA testing under an agreement with the Saigon Zoo.
- The WWF-Cat Tien National Park Conservation Project which would provide financial support and technical advice based on contacts with the IUCN-SSC Crocodile Specialist Group.
- At a later stage, the MARD of the Vietnam Government joined as a stakeholder when they made an additional budget available.

**GOAL, OBJECTIVES AND PLANNED ACTIVITIES**

By late 1999, the following set of objectives were formulated and agreed by the stakeholders to guide the re-establishment programme. The goal to re-establish a population of Siamese crocodile in Cat Tien National Park is to ensure that an ecosystem that is as complete as possible and which represents a natural southern Vietnamese lowland ecosystem will remain as an example for future generations. The objectives to reach this goal are as follows:

1. To re-establish Siamese crocodile in Cat Tien National Park in a careful and scientifically sound manner.
2. To maintain a viable wild population of Siamese crocodile in Cat Tien National Park.

In order to reach the above objectives, aiming at achieving the above goal, a number of activities have to be deployed.

To re-establish Siamese crocodile in Cat Tien National Park in a careful and scientifically sound manner.

- A **feasibility study** has to be executed, assessing the suitability of - and food-availability in the prospective area to host Siamese crocodile, i.e. Bau Sau wetland complex in Cat Tien National Park. The study should include an assessment of impacts of crocodile on the remainder of the ecosystem as well as an assessment on whether crocodiles in the area will be safe from poaching. Of concern is the heavy under-water vegetation which can hamper the movement of young crocodiles. Also the risk of having crocodiles leaving the National Park through the Dak Lua creek, during high water levels and over land has to be assessed.

- The founder population has to be checked on being pure Siamese crocodile breed. Apart from Siamese crocodiles, breeding farms in Vietnam hold large numbers of Cuban crocodiles (*Crocodileus rhombifer*) as well. *C. siamensis* and *C. rhombifer* are known to produce fertile offspring. Release of crocodiles into the wild is only acceptable if pure *C. siamensis* are used. Although there are a number of exterior signs distinguishing *C. siamensis* and *C. rhombifer* (CITES, 1995), second and third generations are hard to distinguish from pure or mixed breeds. Therefore, a **DNA analysis** is essential to ensure that pure *C. siamensis* stock is being used in the re-establishment programme. If this is not done, Cat Tien National Parks runs the risk of ending-up with a crocodile population of unknown composition, which may have far-reaching (negative) ecological effects.

- At least two **staff** of Cat Tien National Park have to receive a minimum 2-month **training** in crocodile handling at the private crocodile farm and the Saigon Zoo.
• Crocodiles transferred to Cat Tien National Park will be held in a temporary facility at the head quarters. Here they will gradually be weaned from saltwater fish and will get used to live freshwater fish.

• Only after completion of the feasibility study, DNA analysis and when the crocodiles are used to fresh water fish, the animals will be released in the Bau Sau wetland complex.

To maintain a viable wild population of Siamese crocodile in Cat Tien National Park.

• **Strict and effective protection** must be ensured prior to a complete release in the wild. With a guard station at Bau Sau, basic facilities are available. However, continued entrance of fishermen into the Bau Sau wetlands complex (who use various kinds of gear including hook lines and nets) is a point of great concern. Released crocodiles may get entangled in the fishing gear and drown if not purposely hunted by poachers. Therefore, a strict control of the area by the Cat Tien National Park Forest Protection Department staff is a prerequisite for the implementation of this programme.

• **Monitoring** of released crocodiles (numbers, dispersment) has to be continued over an extensive period of time.

• **An information campaign** has to be held amongst the people living in the vicinity of the Bau Sau wetland complex (i.e. Dak Lua Commune) and amongst visitors to the National Park. This campaign should aim at disseminating general information about the crocodiles, their value as a member of the National Park’s ecosystem and at avoiding possible crocodile-human conflicts.

• **Small-scale tourism** facilities should be established in the Bau Sau area. These could be a canoe and boardwalks along parts of the perimeter of the wetland. These should facilitate safe crocodile viewing opportunities. In order not to disturb the animals too much and not to put too much pressure on the fragile Bau Sau wetland ecosystem, only small groups of a maximum of 10 people per day should be allowed to visit the Bau Sau area. Special fees should be levied to permit visitors entering the Bau Sau area. The fees should be utilised to maintain strict protection and tourism facilities.

**PROGRESS AND EXPERIENCES SO FAR**

In early 2000, two staff of Cat Tien National Park were trained in crocodile handling at the crocodile farm. A holding cage for the crocodiles was built at the headquarters of Cat Tien National Park. On October 25, 2000 a handing-over ceremony took place in Ho Chi Minh City whereby the Park received 25 crocodiles from Hoa Ca Crocodile Farm. All of them were born in 1998. Saigon Zoo took the responsibility of taking samples for DNA testing to be sent to Queensland University and tagging the individual crocodiles with a micro-chip so that individuals can be recognised when matching test results with individual crocodiles. Unfortunately the samples were not sent to Australia before the animals arrived in the Park. Also, the crocodiles arrived while a habitat feasibility study had not been executed yet. DNA samples of 20 crocodiles were sent to Australia in November 2000 as part of a larger number of samples taken in southern Vietnam. Meanwhile the Vietnam Government provided support for this activity and the Park bought 15 additional crocodiles of unknown breed from crocodile farms. After arrival in the Park, the diet of the crocodiles shifted from eating dead sea-fish to dead freshwater fish, then to live freshwater fish over a period of 2 months.

Members of the IUCN-SSC Crocodile Specialist Group visited the Park in May 2001 and assessed the intended release site (Crocodile Lake) and the different ideas held by different stakeholders on how to proceed with the re-introduction programme. Their expert opinion was discussed with Park and Project authorities and it was concluded that the following line of action was to be followed.

• All crocodiles will have to be DNA tested. Non-pure *Crocodylus siamensis* have to be taken out of the release programme.

• There is no need to buy more crocodiles as the stock available should be adequate to re-populate the wetlands in Cat Tien National Park. Also, buying additional stock is likely to bring non-pure *C. siamensis* to the Park as there are few pure-bred animals available in Vietnam.

• While awaiting DNA test results, the crocodiles should be kept at the Park’s headquarters. Young individuals and DNA tested animals have to be separated from older and un-tested animals. Therefore two additional cages have to be build at headquarters.
• Animals should be released directly into Crocodile Lake and do not need to be kept there in a temporary cage as the habitat at Crocodile Lake is ideal for crocodiles (adequate quantities of fish and no natural predators).

• The best time for release is when flood-waters recede (December – February) and the Crocodile Lake is confined by dry land. As when released, the animals can establish home ranges within a confined area and are more likely to stay there when the next flood increases their potential range.

• In the coming dry season (2001-2002), a group of 10 – 15 animals should be released. The other animals should be kept at headquarters awaiting DNA test results for subsequent releases in 2003.

• The released animals should be monitored using a simple spotlight method. Trials with radio collars (undertaken in May 2001) show that the effort required to locate a signal will render the method inefficient. Additionally, the amount of manpower required to execute a radio-tracking programme is probably not available. Spotlighting should not commence before 10 days after release so that the animals can get used to their new environment undisturbed. Over the subsequent two months, weekly spotlight surveys should be undertaken. After this intensive survey period, the spotlight surveys should be cut back to monthly surveys in order to limit disturbance and to establish a realistic routine within the limited manpower available at the Park.

• The aim for monitoring should be to assess whether the crocodiles remain in Crocodile Lake or whether they will immediately range deeper inside and / or outside the Park. Additionally monitoring information will establish a baseline of the population and will in due time hopefully find a population increase due to natural growth.

The assessment of the habitat and the feasibility for release conducted by the IUCN-SSC Crocodile Specialist Group members confirmed earlier findings (Polet and Tran Van Mui, 1999; Platt and Ngo Van Tri, 2000) that the Crocodile Lake of the Bau Sau wetland complex is an excellent release site. There are no large predators which will cause mortality amongst released crocodiles, fish are available in abundance and the vegetation cover is good. Protection of the area has been greatly improved by stricter control of the Park’s forest protection staff. One concern remaining is the risk that crocodiles can get entangled in abandoned fishing nets floating underwater in the lake.

In June 2001, DNA test results came back from Queensland University. A detailed description of findings is being presented elsewhere (Fitzsimmons, et al. in press). One of the animals held in Cat Tien National Park was proven to be a cross between *C. siamensis* and *C. rhombifer*, despite care taken by the crocodile farmer to keep proper stud-books. This animal has been removed from the release programme.

On December 18, 2001 the first batch of 10 crocodiles were released in the Bau Sau wetland complex. On March 12, 2002 five more animals were released and on March 13, 2002 the last four of the DNA tested animals were released (Table 1). At the time of release the animals were about 3.5 years old and measured 1.55 to 1.92 metres.

<table>
<thead>
<tr>
<th>Release Date</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>December 18, 2001</td>
<td>5</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>March 12, 2002</td>
<td>2</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>March 13, 2002</td>
<td>1</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>8</strong></td>
<td><strong>11</strong></td>
<td><strong>19</strong></td>
</tr>
</tbody>
</table>

**POST RELEASE MONITORING**

**Methods**

Monthly spotlight surveys are used as a baseline index of the crocodile population in Bau Sau (Crocodile Lake). Every month a two-man team, consisting of an observer and boatman, circumnavigate the lake searching for the eye-shine of crocodiles following the methods described by Messel et al. (1981), Ratanakorn et al. (1994), and Perran Ross (pers. comm.). Each survey is carried out as close to the new moon as possible as crocodiles are more wary on the full moon (Perran Ross pers. comm.). Before the start of each survey data on
the lake level, cloud cover, wind, air and water temperature are recorded, as these variables can affect crocodile observability (Woodward and Moore, 1993; Pacheco, 1994).

In 2002 the monthly spotlight surveys can be separated into two phases where alterations to the method were made in May. In the first phase (January-April) the two-man team would circumnavigate the whole lake using a Q-beam spotlight. In May three members of the CSG (Paul Moler, C. L. Abercrombie, and Phil Wilkinson) visited Bau Sau and suggested circumnavigating each of the two lobes of the lake separately and using a weaker spotlight that would not wash out the eye-shine of any nearby crocodiles. In the second phase (June-current) these suggestions have been incorporated.

Results

For the first two monthly surveys there was a low number of crocodiles observed with one or two seen per survey (Table 2). In March, when another 9 animals were released in Bau Sau, the number observed increased sharply. From April to September the number of crocodiles seen each survey has been between 3 to 6 (Table 2), which represents 16 to 32% of a total released population of 19 (Figure 1). Crocodiles have mainly been observed in the smaller lobe, closest to the forest guard station, which is deeper. In February one crocodile has been seen in the large lobe of the lake, and two at the same location in September, which is characterised by large shallow areas of tall reeds around its perimeter. The greater distance travelled by canoe in September was because of the higher lake level after flooding at the end of August.

Table 2. The number of Siamese crocodiles observed, km travelled, number of crocodiles observed/km travelled, and % of the total released population observed during monthly spotlight surveys at Crocodile Lake, Cat Tien National Park, in 2002

<table>
<thead>
<tr>
<th></th>
<th>Number of crocodiles observed</th>
<th>Km travelled</th>
<th>Number of crocodiles observed/Km travelled</th>
<th>% of the total released population observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>1</td>
<td>5.5</td>
<td>0.18</td>
<td>10</td>
</tr>
<tr>
<td>February</td>
<td>2</td>
<td>5.5</td>
<td>0.34</td>
<td>20</td>
</tr>
<tr>
<td>March</td>
<td>6</td>
<td>5.5</td>
<td>1.10</td>
<td>32</td>
</tr>
<tr>
<td>April</td>
<td>3</td>
<td>5.5</td>
<td>0.55</td>
<td>16</td>
</tr>
<tr>
<td>May</td>
<td>5</td>
<td>5.5</td>
<td>0.92</td>
<td>26</td>
</tr>
<tr>
<td>June</td>
<td>4</td>
<td>5.5</td>
<td>0.73</td>
<td>21</td>
</tr>
<tr>
<td>July</td>
<td>3</td>
<td>5.5</td>
<td>0.55</td>
<td>16</td>
</tr>
<tr>
<td>August</td>
<td>3</td>
<td>5.5</td>
<td>0.55</td>
<td>16</td>
</tr>
<tr>
<td>September</td>
<td>6</td>
<td>7.2</td>
<td>0.83</td>
<td>32</td>
</tr>
</tbody>
</table>

Figure 1. The percentage of the total released population of Siamese crocodiles observed during monthly spotlight surveys at Crocodile Lake, Cat Tien National Park, in 2002
DISCUSSION

The 10 to 32% of the crocodile population observed in Bau Sau is comparable to other spotlight studies with a known population size where 9 to 19% of the population was observed (Woodward et al., 1996). This suggests that the spotlight surveys are a suitable index of the local crocodile population. The small variance in the observed number of crocodiles between months indicates a relatively stable population. The high count of crocodiles in March was soon after the second release and was probably influenced by newly released crocodiles still habituating to their new environment. The high count in September was when the lake level had risen above some of the shoreline vegetation potentially improving the chances of seeing crocodiles. The September count also suggests a stable population in Bau Sau and no crocodiles have emigrated to other adjoining wetlands and the Dong Nai River that connect with Bau Sau during flooding at the height of the monsoon season (August-September). The more crocodiles observed in the smaller lobe of the lake is possibly a preference for the deeper water for easier feeding, or because crocodiles were missed in the larger lobe of the lake where the tall reeds reduced visibility.

Spotlight surveys have been an easy method to implement because their simplicity and low time-commitment have allowed them to be incorporated into busy existing schedules. However, as observers have changed, with monitoring activities being transferred to park staff and with changes in park staffing, results cannot be reliably used for any analysis of trends in the observed population (Woodward and Moore, 1993) until standardised observers are maintained at the park. Maintaining standardised observers (from changes in staffing), and a monthly routine, are the focal areas for the future of crocodile monitoring by Cat Tien National Park staff.

FUTURE PLANS

On August 1, 2002, the Park and a new crocodile farmer signed an agreement in which the Park is to receive 100 crocodiles over a period of three years. Samples for DNA testing of these animals were taken on last August 29. A CITES export permit has been applied for and the samples will be sent to Canberra University – Australia for DNA testing. A new batch of 30 to 40 animals is scheduled to be released during the coming dry season (December 2002 – March 2003).

As responsibility for monitoring is being transferred to park staff, monthly spotlight surveys should continue, executed by Park staff, with the aim to detect population trends and habitat use. It is hoped that young crocodiles will be encountered which would prove natural growth of the population. It will also be interesting to see whether there are indications of crocodiles having moved-out of the area after the flood season or whether some crocodiles maintained their home range at the lake despite their larger potential range during the floods.

LESSONS LEARNED

Some lessons can be learned from the experience gained in the crocodile re-establishment programme in Cat Tien National Park – Vietnam.

The programme has a wide range of different partners; from the private sector to governmental organisations to international conservation organisations and specialists. This set-up has its strengths and weaknesses. Most of the expertise and logistical support for the programme is available amongst its partners. However, working with so many different organisations, each with different priorities and with different powers, is a complicated matter. Working towards the success of the re-introduction programme depends on each partner’s willingness to contribute and accommodate other partner’s points of view. This can only be achieved, and geared towards getting results, if the objective of the re-introduction programme is spelt-out right from the start of the activity. This has been the case in the Cat Tien National Park re-introduction programme and well defined goals and activities were formulated at the beginning of the programme.

But even with such clearly defined activities and timetables, different implementation sequences were followed in Cat Tien National Park. The crocodiles arrived in the Park before DNA test results were obtained. An informal feasibility study of the release site was conducted after the animals arrived in the Park. This experience illustrates on-the-ground complexities to implement a programme according to agreed timetables and in a scientifically sound manner. It is due to the partners willingness to consider and re-consider different ideas and priorities that this specific programme has not resulted in the pre-mature release (i.e. crocodiles which have not been confirmed to be pure C. siamensis through DNA analysis) of crocodiles in Cat Tien National Park.
The need to conduct DNA analysis is also evident from the experience in Cat Tien National Park. Although the crocodile farmer kept a stud-book and was convinced that his crocodiles were pure *C. siamensis*, DNA testing concluded that 1 of the 20 tested animals was in fact a hybrid of *C. siamensis* x *C. rhombifer*. If DNA testing would not have been conducted, this animal would have been released and thus an alien species would have been introduced in the Park’s ecosystem.

Spotlight surveys are a suitable index of the crocodile population at Bau Sau as the results in 2002 are comparable to other studies of a known population. Spotlight surveys indicate a stable population of released Siamese crocodiles in Bau Sau before and after the height of annual flooding of the Bau Sau wetland complex (though more surveys are required to assess the post-monsoon population).

Spotlight surveys have been an easy method to implement because their simplicity and low time-commitment have allowed them to be incorporated into busy existing schedules. The only possible problems for the future of monitoring in Cat Tien National Park is maintaining a monthly routine, and non-standardized observers from rapid changes in park staffing.

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The Current Status of the Philippine Crocodile, 
*Crocodylus mindorensis* Schmidt, in the Wild

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**ABSTRACT:** We are currently monitoring the population status of *Crocodylus mindorensis* in the wild. This paper presents the results of population surveys we conducted from 1999 to 2001. We discovered three previously unrecorded populations of *C. mindorensis* in Abra Province and Isabela Province, Luzon Island, and Bukidnon Province, Mindanao Island. We did not encounter crocodiles in Busuanga and Negros Islands. Crocodiles are present in Agusan Marsh, Mindanao Island, but we were not able to identify the species. Our research indicates that there are viable populations of *C. mindorensis* remaining in the wild.
The Status and Conservation of the Philippine Crocodile *Crocodylus mindorensis* in the Northern Sierra Madre, Luzon, the Philippines

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**ABSTRACT:** The Philippine crocodile *Crocodylus mindorensis* is an endemic freshwater crocodile. *C. mindorensis* is the most severely threatened crocodile species in the world, caused by over-hunting and the alteration of its habitat. A previously unknown population was found in the Northern Sierra Madre on Luzon in 1999. At this moment, 7 distinct localities are known with confirmed *C. mindorensis* presence in the Northern Sierra Madre. A total of 41 crocodiles have been found in these localities. In 3 of these sites, successful breeding has been confirmed. The Philippine crocodile seems to be a generalist in the choice of habitat. It is found in fast-streaming mountain rivers, small lakes, stagnant lowland creeks and even in coastal habitats. The locality with the highest human disturbance also has the highest number of crocodiles. Hunting and killing of crocodiles is the main reason for its very low population size in Northern Luzon. The Northern Sierra Madre Natural Park – Conservation Project set up a conservation program which included awareness raising campaigns and meetings with local residents to design a co-management system to protect the crocodiles and their habitat. The support was won of the local government of San Mariano which declared *C. mindorensis* their flagship species and established the first ever Philippine crocodile sanctuary. These initial positive results have led to a proposal to extend the conservation program to a larger area, for a longer period. Whether the used approach is successful on the long term will be closely monitored.

**INTRODUCTION**

**Crocodiles in the Philippines**

There are two species of crocodiles in the Philippines, the Estuarine crocodile *Crocodylus porosus* and the Philippine crocodile *Crocodylus mindorensis*. The Philippine crocodile is an endemic species, it occurs only in the Philippines. The Estuarine crocodile is widespread from Northern Australia to India and although it is threatened in the Philippines it is still common in several of these other countries.

The Philippine crocodile is a small crocodile generally living in inland lakes and the headwaters of rivers. The Estuarine crocodile lives in brackish water, sea and lower river systems. The Philippine crocodile can reach a maximum length of about 2.5 m while the Estuarine crocodile can grow up to 6 m. Apart from size and habitat, the best identification characteristic is the presence of enlarged scales in the neck of the Philippine crocodile. The Estuarine crocodile has a smooth neck.

**Status and conservation of the Philippine crocodile**

The Philippine crocodile is listed in the IUCN Red List (Hilton-Taylor, 2000) as critically endangered (a continuing declining population of fragmented sub-populations in declining areas of occupancy, an adult population of less then 250 individuals, and a population decline bigger than 80 percent in 3 generations). Philippine crocodiles are protected under Philippine law (WCSP, 1997). International trade in Philippine crocodiles is banned under Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (CITES, 1998).

The wild population was estimated at 1,000 individuals in 1982 (Ross, 1982) and at 100 non-hatchling individuals in 1993 with Mindanao and possibly the Sulu archipelago as the last remaining stronghold of the species (Ross, 1998). That was before the rediscovery of the species in Luzon. Because of the continuing adverse security situation in these areas, there is little hope for effective conservation of the Philippine crocodile.
in Mindanao and Sulu. The discovery of the Philippine crocodile in the Sierra Madre, however, offers new possibilities for conservation and survival of the species in the wild.

Conservation initiatives

In 2000, the Philippine Crocodile Recovery Team was created. Its members include officials of the Department of Environment and Natural Resources (DENR), the Director of the Palawan Wildlife Rescue and Conservation Center (PWRCC), which is a captive breeding facility for *C. mindorensis*, and several persons that are professionally involved with *C. mindorensis* conservation or captive breeding. The recovery team prepared a national recovery plan for the Philippine crocodile (Banks, 2000). The primary goals of this recovery plan are to re-establish viable wild populations of *C. mindorensis* and to ensure its long-time survival. The IUCN/SSC Crocodile Specialist Group recommended in 1998 that captive breeding offers the best chance for the species’ survival (Ross, 1998). A large number of *C. mindorensis* have been bred in the PWRCC but so far no crocodiles have been reintroduced to the wild. It must be noted that both the IUCN Crocodile Action Plan (Ross, 1998) and the Philippine Crocodile Recovery Plan (Banks, 2000) do not include the here presented information on *C. mindorensis* in the Sierra Madre as these data have only been gathered during the last two years. A new priority in *C. mindorensis* conservation might now be the identification and study of other sites in Northern Luzon and conservation and recovery of these wild populations.

The Northern Sierra Madre

The Sierra Madre mountain range runs from the Northeastern tip of Luzon all the way south to Quezon province near Manila. The portion in Northeastern Luzon is called the Northern Sierra Madre. The highest summits are about 2,000 meters above sea level. On the eastern side, the mountains dip steeply into the Pacific Ocean, sometimes with small coastal plains and valleys that are sparsely inhabited. On the western side in Northern Luzon, below a steep ridge, a rolling hilly landscape can be found into the Cagayan Valley. Cagayan river is the largest river of the Philippines and is fed by run off from the Sierra Madre mountains in the West and the Cordillera mountains in the East. Annual precipitation in Cagayan Valley is about 2,000 mm. There is no distinct dry period although there is much less rain from March to June. Most rain falls during typhoons, which strike the area yearly between July and November. Because the Sierra Madre is so steep, the area escaped large scale commercial logging in higher elevations during the logging boom in the Philippines of the 1960’s and 70’s. Lower areas however have been logged over extensively. Upland farmers followed the clearing of the land and established themselves in the foothills of the Sierra Madre during the past 40 years. Before that time the area was sparsely inhabited by the Agta, an indigenous hunter/gatherer people.

The remaining forest cover of the Sierra Madre attracted the attention of conservationists. In 2001 the portion of the Sierra Madre mountains in Isabela province was declared a protected area: the Northern Sierra Madre Natural Park (NSMNP). It is the largest protected area of the Philippines with an area of about 360,000 Ha. It is also one of ten priority sites for biodiversity conservation in the country and several international NGOs have started conservation projects in the area.

The Northern Sierra Madre Natural Park – Conservation Project (NSMNP-CP)

The NSMNP-CP is funded by the Dutch government and implemented by Plan International, an organization better known for its child-focused projects. The project started in 1996 and the first phase will end in October 2002. Most probably it will then continue in a second phase, with another implementer. The main objective of the NSMNP-CP is to assist the Philippine government with biodiversity conservation in the Northern Sierra Madre through biodiversity studies, awareness raising, alternative livelihood development and setting up (co-)management structures of natural resources and the park itself. The biodiversity research component consists of a flora, marine and fauna team. In March 1999, Samuel Francisco, a local fisherman of the small village of San Isidro in the periphery of the NSMNP, accidentally caught a hatchling crocodile which was turned over to field staff of the NSMNP-CP. The hatchling was identified as *Crocodylus mindorensis*, which was later confirmed by a team from the PWRCC. Following the discovery, the fauna team of the NSMNP-CP started to look for remaining wild populations of the Philippine crocodile in the Northern Sierra Madre. Once these populations were found, all components of the NSMNP-CP were mobilized to work on their conservation.
METHODS

Since the discovery in 1999, a number of crocodile surveys have been carried out in the Northern Sierra Madre by the NSMNP-CP. Two of these surveys were conducted together with co-workers of the PWRCC and Frederick Pontillas. Two in-depth studies were carried out by Dutch MSc. students in co-operation with the Cagayan Valley Program on Environment and Development (CVPED), which in its turn is a scientific co-operation program between Isabela State University and the University of Leiden. Recently, surveys are also being carried out by students under the CROC project (Crocodile Research, Observance and Conservation) which is funded by British Petroleum and implemented by CVPED. The data presented in this paper is a summary of the results of these studies (Pontillas, 2000; Tarun, 2000; Van Weerd, 2000a; Van Weerd et al., 2000a; Van Weerd, 2000b; Tarun, 2001; Van Weerd et al., 2001; Oppenheimer, 2001; Oudejans, 2002; Tarun and Guerrero, 2002; Van Alphen and Telan, 2002).

Interviews were carried out in all settlements of the Northern Sierra Madre Natural Park (NSMNP) to gather secondary information on current and historic presence of crocodiles. Information on current presence was checked in the field, often by hiring the informant as guide and visiting the sites he or she mentioned. Day light track searches were carried out along riverbanks as well as night surveys using strong flashlights. Of crocodiles observed, size was estimated and individuals were placed in the following categories: (1) hatchling (very small crocodiles up to 0.3 m), (2) juvenile and sub-adult (0.3 to 1.5 m), and (3) adult (longer than 1.5 m). Night surveys were repeated and the maximum number of one night was taken as population count. Secondary information on crocodile numbers that could not be confirmed in the field, or of sites that could not be visited, was categorized as “estimated” if the information was given by several independent informants and sounded reliable. Habitat was mapped and described following a standard protocol. The results presented here are a brief summary of the main habitat characteristics.

PHILIPPINE CROCODILE DISTRIBUTION AND POPULATION SIZE
IN THE NORTHERN SIERRA MADRE

In 1999, the presence of *C. mindorensis* was confirmed in the Northern Sierra Madre (van Weerd, 2000). This area was previously identified as a probable *C. mindorensis* locality based on secondary information (Ross, 1982) but hard evidence was lacking. A thorough survey of wildlife species of the area during the early 1990’s, of which the spectacular results certainly helped to establish the park, had not recorded the Philippine crocodile for the Northern Sierra Madre (NORDECO and DENR, 1998).

Estuarine crocodiles are still present in coastal wetlands on the eastern side of the Sierra Madre, though in very small numbers (NORDECO and DENR, 1998; Oppenheimer, 2001; Van Weerd, 2001). However, *C. mindorensis* was also observed near and even in the ocean. One specimen was captured leading to a positive identification (van Weerd, 2000) and another adult *C. mindorensis* was caught by fishermen in a mangrove area in May 2001 and photographed. Within the municipality of San Mariano there are 6 localities with confirmed Philippine crocodile presence. The total population ranges from 41 confirmed individuals in these 6 localities (Tarun and Guerrero, 2002) to an estimated 77 based on secondary information (Oppenheimer, 2001), and probably more than 100 in a larger area including the Cordillera part of Cagayan Valley (Oudejans, 2002). However, recent surveys conducted by van Alphen and Telan (2002) suggest that *C. mindorensis* can no longer be found in many of these localities. 26 hatchlings, 8 juveniles and 7 adults were observed. *C. mindorensis* has been confirmed breeding in 3 sites: Lake Dunoy, Disulap River (in 2000) and Dinang Creek.

At several other localities in San Mariano, crocodiles have been observed but these are probably not breeding areas because hatchlings were never observed. Two localities long suspected to hold significant *mindorensis* populations, based on interview results, in and near San Mariano were surveyed in July 2002: Abuan River and the upper stream of Ilaguen River. Unfortunately no crocodiles were found and disturbance by illegal loggers/hunters along Abuan river is of such a magnitude that it is unlikely that a significant population of crocodiles can survive here. Ilaguen river remains a suspected site since the habitat seems to be very suitable for crocodiles: large deep ponds and little disturbance. But, during the July 2002 survey no crocodiles or tracks were found.

Lake Dicatian and surrounding creeks in the coastal municipalities of Maconacon and Divilacan are confirmed as *C. mindorensis* localities (Oppenheimer, 2001) although reliable population estimates are lacking.
Fishermen caught two adult Philippine crocodiles in the Pacific Ocean at the mouth of creeks in this area. Both crocodiles died.

Table 1 shows the confirmed population size per age class in the various localities as well as localities that are suspected to harbor crocodiles but which could not (yet) be confirmed. Localities that were visited based on secondary information but which surely do no longer hold crocodiles are also shown. Most of these localities were very recently visited as part of a survey program under the CROC Project. Map 1 shows the localities with confirmed or suspected Philippine crocodile presence in and around the NSMNP. There are two distinct sub-populations: (1) Lake Dicatian and surrounding rivers in Divilacan, and (2) Ilaguen River and its tributaries and lakes in San Mariano and Ilagan. The numbers placed before localities in Table 1 refer to the same location numbers in Map 1.

**Map 1**: Philippine crocodile locations in and near the Northern Sierra Madre Natural Park. Numbers correspond with locality numbers in Table 1.

**Table 1.** Identified Philippine crocodile localities and confirmed population size per age class as well as suspected crocodile localities and localities which do no longer hold crocodiles. Localities in bold font are confirmed to hold crocodiles. Numbers refer to localities in and near the NSMNP and are equal to numbers in Map 1.

<table>
<thead>
<tr>
<th>Location</th>
<th>Hatchling</th>
<th>Juvenile/sub-adult</th>
<th>Adult</th>
<th>Total</th>
<th>Site visited but no crocodiles anymore</th>
<th>Site visited, no crocodiles observed but suspected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cagayan Valley, NSM</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Isabela Province</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Abuan River</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Kamalaklakan</td>
<td></td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Pagsungayan</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Lake Dungsog</td>
<td></td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Lake Dunoy</td>
<td>12</td>
<td></td>
<td>2</td>
<td>14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Disulap River</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Disabungan River</td>
<td></td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8. Dinang creek</td>
<td>14</td>
<td>6</td>
<td>2</td>
<td>22</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Oudejans (2002) identified several other localities in the Cordillera mountains, outside the coverage area of the NSMNP-CP, with possible *C. mindorensis* populations on the basis of interviews. These are Magat River with an estimated total of 10 crocodiles and Siagot River with another 10 crocodiles. These localities were not yet visited to confirm the presence of crocodiles. The fact that new crocodile localities were identified during many of the surveys in new areas, and the fact that Philippine crocodiles are easily overlooked, lead to the conclusion that *C. mindorensis* might very well still occur in low numbers in many localities in North Luzon.

During the recent surveys of Van Alphen and Telan (2002) however, no new areas were found and most informants mention recent local disappearance of crocodiles in sites visited.

### Habitat

Detailed habitat characterization studies were carried out in Lake Dunoy, Disulap river and Dinang creek in January to March 2001 (Oppenheimer, 2001). Table 3 and 4 summarize the findings.

#### Table 3. The general characteristics of Dunoy, Diwakden and Dinang

<table>
<thead>
<tr>
<th>Location</th>
<th>Wetland Type</th>
<th>Size</th>
<th>Turbidity</th>
<th>Flow</th>
<th>Banks</th>
<th>Human activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dunoy</td>
<td>Lake</td>
<td>100 x 50 m</td>
<td>Clear, vegetated</td>
<td>Stagnant</td>
<td>Not steep, dense vegetation of shrub and trees</td>
<td>Slash and burn farming, rice paddies nearby. No fishing.</td>
</tr>
<tr>
<td>Disulap</td>
<td>River</td>
<td>Average width: 24 m</td>
<td>Clear</td>
<td>Rapid</td>
<td>Cliffs and pebble beaches, cliffs forested</td>
<td>Few cultivated fields, moderate fishing/hunting activities</td>
</tr>
<tr>
<td>Dinang</td>
<td>Creek</td>
<td>Average width: 7 m</td>
<td>Turbid</td>
<td>Nearly stagnant, small rapids</td>
<td>Steep clay banks, small strip of shrub</td>
<td>Cultivated all along creek. Creek used by bathing cows. Fishing</td>
</tr>
</tbody>
</table>

#### Table 4. Physical characteristics of Dunoy, Diwakden and Dinang in the period January to March 2001.

<table>
<thead>
<tr>
<th>Location (N)</th>
<th>Temp (°C)</th>
<th>pH</th>
<th>Flow velocity (m/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dunoy (11)</td>
<td>23.0 - 25.0</td>
<td>4.34 - 6.09</td>
<td>0</td>
</tr>
<tr>
<td>Disulap (21)</td>
<td>22.5 - 25.0</td>
<td>6.85 - 7.25</td>
<td>0.01 - 0.67</td>
</tr>
<tr>
<td>Dinang (20)</td>
<td>24.0 - 29.0</td>
<td>6.49 - 7.74</td>
<td>0.02 - 1.55</td>
</tr>
</tbody>
</table>
The variation in habitat characteristics between the sites is striking. *C. mindorensis* occurs in small lakes, fast streaming rivers and stagnant creeks. pH varied from acid (4.34) to slightly basic (7.74). Riverbank substrate and vegetation varied from cliffs with pebble beaches to clay banks with shrub and secondary forest vegetation. Dinang Creek is surrounded by cultivated fields with a very high disturbance level from cultivating farmers and bathing cows. Disulap River is much less disturbed. None of the localities is really secluded or undisturbed. *C. mindorensis* is found in both fresh and sea water environments though the occurrence in the sea has to be studied further and is based on two accidental catches by fishermen in coastal waters. It seems that *C. mindorensis* is much more of a generalist than a specialist and does not totally depend on undisturbed freshwater habitats. Why then is the species so rare?

**Threats**

In the Municipality of San Mariano, Isabela, the decline of the crocodile population is thought to be linked with poaching and destruction of crocodile habitat such as illegal fishing, slash and burn farming up to the edge of rivers and lakes, and deforestation. Many areas where crocodiles historically occurred but disappeared show these human activities. However, in Dinang Creek this theory seems to be debunked as both sides of the creek are intensively cultivated (rice and corn), grasses and shrub along the riverbanks are burned, and fishing activities are regular occurrences. Dinang creek has the highest number of crocodiles of all localities known in the Northern Sierra Madre.

Most respondents of interviews on the reasons of decline of *C. mindorensis* in San Mariano do mention that hunting decimated the former crocodile populations, notably commercial hunting during the 1960s by crocodile hunters from Mindanao (Oudejans, 2001). During the period March 1999 to August 2002, several incidents in which crocodiles were captured or killed were reported. Two adult Philippine crocodiles were accidentally caught by fishermen in the coastal waters of Isabela and died after being kept tied to ropes for weeks. The DENR, responsible for the release or confiscation of captured Red List species, was not able to convince the fishermen to release the crocodiles and did not enforce the law. Several juvenile crocodiles were caught in San Mariano and sold as pet. They could not be retrieved, as the source did not want to disclose the names of clients. At least one adult crocodile was killed in Dinang creek out of fear or ignorance. Another adult crocodile was killed here in July 2002 by the Philippine army and eaten as snack. One juvenile crocodile was caught in Ilaguen River and kept as pet.

It seems that killing and capturing of crocodiles is the main reason for the continuing decline of *C. mindorensis* in Northern Luzon, and probably the Philippines as a whole. Habitat alteration and food competition might play a role as well but less so then hunting. Currently, the remaining population of *C. mindorensis* in the Northern Sierra Madre is also threatened by fragmentation and by being too small. Stochastic effects (flashfloods, extreme droughts, reduced chances to find a mating partner) and genetic effects (inbreeding) become large threats in very small populations.

Because of its shy nature and small size, the Philippine crocodile offers no real danger to humans. Indeed, in all localities where crocodiles are found in San Mariano, they share the river and natural resources with humans living nearby. There are no reported attacks of Philippine crocodiles on humans from direct sources. All stories about crocodile attacks are “hear-say” and could refer to attacks by Estuarine crocodiles, which are believed to have been present in Cagayan river until fairly recently (Oudejans, 2002). In the San Mariano area all crocodiles present are Philippine crocodiles. Acceptance of co-habitation with crocodiles and sharing of freshwater habitats might therefore be easier to achieve compared to areas where crocodiles pose a danger to people. Fighting ignorance by providing information and winning the support of the local farmers, fishermen and hunters is of utmost importance for a successful conservation program.

**CONSERVATION OF THE PHILIPPINE CROCODILE IN SAN MARIANO**

In San Mariano, *C. mindorensis* is mainly found outside the NSMNP and its buffer-zone. A conventional conservation program based on minimizing people-crocodile interactions and totally protecting natural crocodile habitats can therefore not be employed. Removing people from the crocodile inhabited areas is, in our time, no longer a socially acceptable option and would not be accepted by the local population and local government. It
would also work counter-productive as local inhabitants would start to see the crocodiles as a threat to their livelihood and law enforcement in protected areas in the Philippines is currently generally lacking.

Therefore, any long term conservation and protection program for *C. mindorensis* will have to employ a co-management approach wherein all stakeholders play a serious role and share responsibilities. A long-term program should definitely include mitigating measures to lessen the impact of anthropogenic factors, which will always be present at various intensities but it should also include benefits for affected local communities to solicit their active support and compensate for any adverse impact.

After the discovery of *C. mindorensis* in San Mariano in 1999, a short-term conservation plan was prepared and executed by the NSMNP-CP and the Local Government Unit (LGU) of San Mariano from July 2000 to May 2002. This conservation program was focused on Disulap River and the surrounding communities of San Jose and San Isidro. Disualp River was the first location with confirmed presence of crocodiles and also the first site where breeding was confirmed. The main goal was to establish a crocodile sanctuary which would be accepted by the local communities. The conservation plan was drafted by the NSMNP-CP but revised with inputs from local communities who formally accepted the final version. The proposal was also presented to the Protected Area Management Board (PAMB), which is the multi-sectoral body responsible for decisions about the NSMNP, and was subsequently approved. The objectives of this conservation plan were the following:

1. Generating data on Philippine crocodile distribution, population size, basic ecology and threats in the Northern Sierra Madre.
2. Increasing the awareness among the local population with regards to the status and need of protection of the Philippine crocodile.
3. Involving the local population in co-management of the Philippine crocodile and establishment of community declared crocodile sanctuaries.
4. Involving all stakeholders in planning and writing of a long-term action plan for the conservation of the Philippine crocodile in the Northern Sierra Madre and securing funding for the execution of a long-term conservation plan.

To increase the support of local communities an integrated conservation and development approach was used with attention and budget for the provision of alternative livelihood options to target communities.

**Activities conducted leading towards co-management and sanctuary establishment**

**Information, Education, Communication (IEC)**

Information campaigns were conducted with the objective of educating the people on the nature and status of the Philippine crocodile and its possible imminent extinction, if conservation and protection efforts would not be implemented immediately. 5 awareness sessions were held in the villages of San Isidro and San Jose. Posters, produced by the NSMNP-CP, were used during these sessions, which were left behind in the community for display.

Two thousand flyers in Tagalog were produced as well as colored posters (1,000 in English and 1,000 in Tagalog), which were distributed to all villages in and near the NSMNP. Additional copies were given to the People’s Organizations (PO) for distribution to people passing by their villages. The Philippine crocodile has been featured several times in the Tagalog newsletter that the project is distributing among local communities and in radio broadcasts on popular local radio stations. A comic album on environmental issues was produced and distributed featuring a story about the Philippine crocodile. *C. mindorensis* is one of the topics of the community theatre groups (*Dalaw Turo*) that were established in the Sierra Madre by the NSMNP-CP and the DENR. The general theme of the campaigns was “the Philippine crocodile, something to be proud of”. The mayor of San Mariano took the initiative to have t-shirts printed with this slogan in Tagalog and with a picture of *C. mindorensis* to present to visitors of his town.

**Community dialogues and public consultations**

Following the IEC sessions, a proposal for a Philippine crocodile conservation program was drafted. The draft proposal was discussed with the community residents of San Isidro and San Jose during meetings and informal discussions. The need to regulate human activities within the proposed sanctuary and the need to form
a community protection group were discussed. Both got the approval of the local residents. The residents came with suggestions to balance the need to have transportation access and some fishing activities with crocodile conservation within the proposed sanctuary. This resulted in well-defined areas within the sanctuary where regulations became site-specific. After the public consultation sessions, attendees were given survey forms wherein they could signify whether they were in support of the Philippine crocodile conservation program or not. The proposal got an overwhelming support both in San Isidro and San Jose.

**Lobbying for local government support**

When the first retrieved hatchling was identified as the Philippine crocodile, the LGU of San Mariano was informed and provided with an orientation on the need of its conservation. The LGU responded immediately and passed several ordinances in support of Philippine crocodile conservation.

Following the public consultation sessions in San Isidro and San Jose, the LGU of San Mariano held a committee hearing wherein all the queries on a proposed ordinance to declare a sanctuary were explained and clarified. Additional public consultations were then conducted by the LGU. The draft copy of the ordinance was discussed and the map of the proposed sanctuary was shown to the local stakeholders. Getting the approval from the community residents living near the sanctuary, the ordinance was passed and approved by the LGU of San Mariano on September 7, 2001.

The following ordinances and resolutions were passed and approved by the LGU of the Municipality of San Mariano, Isabela:

1. Ordinance No. 99-025: an ordinance identifying the Philippine crocodile as an endangered species occurring in San Mariano and prohibiting the collection and annihilation of *C. mindorensis* (Municipality of San Mariano, 1999).
2. Ordinance No. 2000-002: an ordinance prohibiting the catching, hunting, collecting, or killing of the Philippine crocodile for pets, sports, collection or personal consumption. This ordinance also declared the Philippine crocodile as the wildlife flagship species of the municipality (Municipality of San Mariano, 2000a).
3. Resolution No. 2000-133: a resolution earnestly requesting the NSMNP-CP and DENR to put up a crocodile rescue center in the municipality (Municipality of San Mariano, 2000b).
4. Ordinance No. 2001–17: an ordinance declaring the identified crocodile areas in sitio San Isidro, Disulap and parts of barangay San Jose, municipality of San Mariano, as Philippine crocodile sanctuary (Municipality of San Mariano, 2001).

**Protection and co-management of crocodile habitats inside and outside the NSMNP**

An environmental management plan for the NSMNP was produced in 2000. This plan includes crocodile habitat management zones in identified crocodile areas within park boundaries. These zones are totally protected and cannot be used for any development purposes (DENR, 2000).

Outside the park, Disulap river is currently the only Philippine crocodile sanctuary. In collaboration with the LGU of San Mariano billboards have been produced and installed along the sanctuary to provide information about the sanctuary and the Philippine crocodile. A community protection group will be set up to protect and control the sanctuary. Alternative livelihood support is being provided by the NSMNP-CP to local residents that are affected by the establishment of the sanctuary.

Disulap River was selected as one of the Biodiversity Monitoring System (BMS) sites, which is the official monitoring system for protected areas in the Philippines. The NSMNP-CP assisted DENR with the development of a crocodile monitoring protocol and the establishment of the BMS in Disulap River.

**Long-term conservation of the Philippine crocodile in the Northern Sierra Madre**

The IEC campaigns, the meetings and consultations, and finally the declaration of the Disulap River Philippine crocodile sanctuary are a first step in the direction of a long-term conservation strategy for *C. mindorensis* in the Northern Sierra Madre. The lessons learned are very useful for a continuation of a co-
management approach to implement this strategy and show that it is possible to win community support for the conservation of threatened species, even if these are crocodiles. The real success can only be measured in crocodiles. The monitoring system, which has been set up, should provide this information.

In May 2002, a workshop was held in Cabagan and San Mariano, Isabela, to design a long-term conservation plan for *C. mindorensis* in Northern Luzon. Stakeholders present included local residents, LGUs, regional and national DENR officials, the Director of the PWRCC and the members of the Philippine Crocodile Recovery Team as well as members of the IUCN Crocodile Specialist Group. The output of this workshop will be a five-year plan, based on the inputs of all stakeholders present, with a comprehensive integrated co-management strategy for development and conservation of crocodile sites and nearby communities in San Mariano. A co-management group is to oversee the implementation of this plan with funding expected to be coming from the Dutch government through the second phase of the NSMNP-CP.

A research proposal was prepared earlier by the Cagayan Valley Program on Environment and Development (CVPED) in collaboration with the NSMNP-CP. The aim of this proposal was to get funding for the involvement of local students of the Isabela State University in crocodile research activities and to extend crocodile surveys in Northern Luzon beyond the coverage area of the NSMNP-CP. This proposal, the CROC: Crocodile Research, Observation & Conservation project (CVPED, 2002), won the British Petroleum (BP) Conservation Program Gold award in April 2002 and research activities funded by this program are currently ongoing (September 2002). Research activities will have to continue during the coming years with a strong collaboration between the DENR, the PWRCC, CVPED, ISU and the NSMNP-CP. Development of a long-term research strategy by these partners was part of the crocodile workshop of May 2002.

The best incentive for the stakeholders to make the conservation and research plan work was the observation of a juvenile crocodile, in full daylight on the bank of Dinang creek, during the field visit of the workshop. Whether this juvenile will once breed in San Mariano depends especially on the people of San Mariano. There is certainly hope that it will.

**ACKNOWLEDGEMENTS**

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ABSTRACT: The last full CSG meeting was held in Cuba, home of the endemic Crocodylus rhombifer, where considerable discussion was devoted to its conservation. Here we present an update on work that has been carried out, as well as plans for future projects, in the two remaining areas for this species, the Zapata Swamp and the Lanier Swamp.
Population Status and Management Guidelines for the Orinoco Crocodile
(Crocodylus intermedius) in the Capanaparo River, Venezuela
(Progress Report)

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ABSTRACT: In order to define management strategies oriented towards the conservation and recovery of the Orinoco Crocodile (Crocodylus intermedius) in the Capanaparo River, the abundance and population structure were determined, including temporal and spatial variations. Night surveys were conducted along 185 km of river between October 2000 and June 2001. Abundance indices between 0.39 and 2.92 individuals/km were recorded, with significant statistical differences between river sections (P < 0.01); the overall mean for all sections was 1.43 individuals/km. The population size was estimated as 536 non-hatchling individuals for all the Capanaparo River basin. No differences were recorded on the population structure between river sections, with a general structure mainly composed by juveniles (58.0%), followed by adults (24.1%), and subadults (17.9%). A significant negative correlation (-0.52, P = 0.0002) between crocodiles and caimans (Caiman crocodilus) in different river sections was obtained. One of the main problems for the conservation of crocodiles at Capanaparo River is the local practice of harvesting eggs and hatchlings. Considering our results, reducing the actual pressure on the species and accomplishing the recovery of this crocodile, may be possible by incorporating local human communities in the conservation efforts in combination with a crocodile release program.

Keywords: Abundance, conservation, Crocodylus intermedius, population structure.

INTRODUCTION

The Orinoco Crocodile (Crocodylus intermedius) is one of the most critically endangered species of crocodile in the world (Thorbjarnarson 1992). Commercial overexploitation from 1930 to the end of 50’s, decimated its populations in most of its original area of distribution (Medem 1983, Seijas 1998). Even though crocodiles have been legally protected in Colombia and Venezuela for almost 30 years, and the international trade has been prohibited by the Convention of International Trade in Endangered Species (CITES) (King 1989), the species is still threatened by a combination of factors including habitat destruction, egg harvesting, incidental and intentional killing, and collection of animals to be sold as pets (Thorbjarnarson & Hernández 1992). Other factors affecting the recovery of the Orinoco Crocodile are related with the expansion of Caiman crocodilus populations, a species which could have some degree of competition with the crocodiles, in particular in those places where C. intermedius maintains very low population levels (Thorbjarnarson & Hernández 1992, Llobet 2002).

The Orinoco Crocodile is present just a small fraction of the territory which represented its original area of distribution. The commercial hunting of this species eliminated the populations from the most of rivers originally occupied by crocodiles. This is the only crocodilian species in the world with a distribution restricted to one basin, The Orinoco River Drainage (Medem 1981, 1983, Thorbjarnarson & Hernández 1992). This basin comprises approximately 1100000 Km², which represents 70% of Venezuelan and 30% of Colombian territory (Lewis 1988, Hamilton & Lewis 1990). Historical information stated that the primary habitat of this species was in the major rivers of the Llanos region of Colombia and Venezuela (Humboldt 1975, Páez 1980, Wickham & Crevaux 1988), especially the Meta, Arauca and Guayavero-Vichada rivers in Colombia, and Apure, Portuguesa, Arauca and Orinoco rivers in Venezuela (Seijas 1998).

Apparently in Venezuela, the Orinoco crocodile populations extended (in low densities) up stream of many Llanos rivers even into surrounding areas close to the foothills of the Andes, and also in some of the southern tributaries of the Orinoco in heavily forested regions of the Cuchivero and Caura rivers (Ramo & Busto 1986,
Thorbjarnarson & Hernández 1992, Arteaga et al. 1994). Unconfirmed information exists about the presence of this species in the Casiquiare and Ventuari rivers. Nevertheless, it is probable that these regions contain very low population levels of crocodiles.

In Venezuela, during the last twenty-five years, scattered individuals and small populations have been reported. However, the most important and probably the only viable populations are found in two very different areas: the Capanaparo River in the state of Apure, and the Cojedes-Sarare system river in the states of Cojedes and Portuguesa. Prior data suggested that a population of more less 1000 individuals could be found in both rivers (Godshalk 1978, 1982, Thorbjarnarson & Hernández 1992, Seijas & Chávez 2000).

The complicated situation of crocodile populations led to the development of an Action Plan (FUDENA 1993) and a Strategic Plan (PROFAUNA 1994), each with a groups of midterm strategies and goals for the recovery of the Orinoco crocodile populations (Program for the Conservation of the Orinoco Crocodile in Venezuela – PCOCV) (Seijas et al. 2001). After eight years of the development of this program (PCOCV), it is considered that the goal of consolidating at least ten viable populations of the species is still to far from being achieved. Except for the Santos Luzardo National Park, and the Aguaro-Guariquito National Park, the situation of the species is not known for certain in the entire Venezuelan system of protected areas. Moreover, there is evidence that small crocodile populations (Tucupido, Anaro, and North Cojedes rivers) are experiencing a serious decrease in size (Seijas et al. 2001), while no actions have been taken to protect the major two populations of the species (Capanaparo and Cojedes rivers), which could not assure, by themselves, the conservation of Crocodylus intermedius in Venezuela.

The crocodile population of Capanaparo River (within Santos Luzardo National Park) still face several threats by egg collecting and the sale of hatchlings, carried out by local people (Thorbjarnarson 1992, Llobet 2002). The importance of this population was previously mentioned by Godshalk (1978, 1982), and confirmed by later research (Thorbjarnarson 1988, Thorbjarnarson & Hernández 1992). These authors emphasized the good habitat conditions of Capanaparo River for the crocodile population, and reported sections of the river with high population densities. Following these results reintroductions of almost 500 non-hatchling individuals, collected previously from the Capanaparo River and raised in captivity for almost a year, were carried out (Arteaga et al. 1997).

After these management actions were occurred, some conflicts between local people and the office in charged of the national parks administration (INPARQUES) started at Santos Luzardo National Park. These conflicts led to the end of the administration of the Park, and blocked any chance to continue with the ongoing conservation activities. This situation probably had a significant effect on the wildlife, and particularly on the crocodile population. The major threat represented bay collecting the eggs and hatchlings (for local consumption and for sale to tourists), was certainly increased due to the lack of administration of the Park. No control mechanisms or conservation activities could be applied as long as the Capanaparo River was not recovered as an in situ conservation area. This situation, continuing for the last ten years, delayed the realization of any effort to accelerate the recovery of the species or to obtain information on the ecology.

Careful and reliable monitoring of crocodile populations is an essential requirement for the implementation of a management program for its conservation. In this study, we attempt to update the population status of C. intermedius in the Capanaparo River and recommend some guidelines for future management actions intended to accelerate the recovery of crocodile populations in the area.

**STUDY AREA**

The Santos Luzardo National Park is located in the southwest Llanos of Venezuela; the northern boundary of the Park is the Capanaparo River. The south border of the Park is the Cinaruco River, the east border is the Orinoco River, and the west border is also the boundary between Achaguas and Pedro Camejo municipalities (Figure 1).

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METHODS

The Capanaparo River is an effluent of Orinoco River and it drains the lowlands of South Apure. Its waters contain an important amount of silts and receive many tributaries with black water (and low productivity) whose origin is in the lowlands. This situation makes the Capanaparo River a mixture between clear waters and black waters (Thorbjarnarson 1988, Thorbjarnarson et al. 1993). Along the river is a gallery forest, often associated with oxbow lakes or old meanders of the river. During dry season, long beaches alternate with deep pools, this situation makes the Capanaparo River a good habitat for crocodiles, it provides a great number of places for basking and nesting. Conductivity varies from 27.1 a 45.3 µS, with an average of 34.5 µS, and the average temperature of water is 29 °C (Muñoz & Thorbjarnarson 2000).

According to data from the Environment Ministry (MARN) of San Fernando de Apure, in the area there is a precipitation range from 1640 to 1644 mm. These data were collected in two stations situated approximately 15 km to the north and 20 km to the south of Capanaparo River respectively, both along the road which connects the cities of San Fernando with Puerto Páez (Fig 1). The dry season occurs from December until March, and the rainy season starts during April producing the higher precipitation level during the month of July. This precipitation regime influences the dynamic of Capanaparo River, which presents the highest water level during August, and the lowest level during April.

From a socioeconomic point of view, the Santos Luzardo National Park has a low human population density, with the presence of some cattle ranches, and communities inhabited by campesinos and indigenous people (most of them belonging to Pume or Yaruro tribe). The livelihoods (beside extensive cattle raising) are basically subsistence activities. The poverty levels of local people (especially indigenous people) are very high.

For the purposes of this study, three sectors of Capanaparo River were selected. The first, called Piedra Azul by the presence of a community with that name, had an approximate length of 45 Km. The second one, called Naure by the presence of that community, also had an approximate length of 45 Km. The third one, called Las Campanas (the community Las Campanas was located in the middle of the sector) had an approximate length of 30 km (Fig. 1).

METHODS

To determine population status of crocodilians at Capanaparo River, night surveys were made from October 2000 to June 2001, using a 12 foot boat powered by a 30 hp outboard engine. Monthly repetitions were made,
surveying approximately a section of 15 km of river each night. The distance of the surveys was measured with the odometer of a Global Positioning System (GPS Garmin 12).

As we stated before, the entire study area was divided into three sectors named Piedra Azul, Naure and Las Campanas due to the nearest human communities. Piedra Azul and Naure sectors were subdivided into three sections each (P1, P2 and P3 for Piedra Azul, and N1, N2 and N3 for Naure). Las Campanas sector was divided into two sections (C1 and C2). Every section of the entire study zone had approximately 15 km length. The complete surveyed length of river was approximately 120 km, within a 185 km section of Capanaparo River (Fig. 1). Due to the characteristics of Capanaparo River, surveys were made first for one shore and then for the other one. Because of the low water level during dry season, it sometimes was not possible to survey the entire 15 km section. Only surveys longer than 10 km were considered for later analysis.

During surveys, a 500,000 candles power light connected to a 12 V battery was used to locate the crocodilians by means of reflective eye shine. All crocodilians sighted were approached as close as possible to allow a positive identification of the species (C. intermedia or the sympatric Caiman crocodilus) and to estimate the body size (total length, TL). In the field, 10 cm size-class intervals were used, but for analyses of size class distribution, 60 cm size-class categories were used (Seijas 1998, Seijas & Chávez 2000):

Hatchling crocodiles (Class I individuals, generally less than 6 months old) and caimans were counted but not considered in this study. Based on previous studies (Seijas 1995, 1998, Seijas & Chávez 2000), non-hatchling crocodiles less than 180 cm in total length were considered as juveniles; crocodiles in Class IV (major than 180 but less than 240 cm in total length) were regarded as sub-adults, and those individuals major than 240 cm in total length were classified as adults. To compare our results with those obtained by Thorbjarnarson & Hernández (1992), a second 50 cm size-class intervals were used. When an individual could not be identified as crocodile (C. intermedia) or spectacled caiman (C. crocodilus), it was placed in a “Not identified” category (NI). These individuals were not considered for the analysis.

The analyses of abundance and population structure were realized considering the results from surveys undertaken from November 2000 to June 2001. The month of October of 2000 was used to investigate the river and to standardize the survey methodology. The relative population abundance index (PI) of crocodilians was expressed as number of individuals per kilometer of river. To analyze how the fraction of crocodiles sighted changes as the dry season progresses, the PI obtained in every survey (individuals/Km) was expressed as a percentage of the PI obtained during April (taken as 100%) in the same river section. April is usually the last month of the dry season, a time when the river reaches its lowest level. This method allows the comparison of results from localities with different PI values. A correlation analysis was used to describe the relationship between these percentages and the days after November 21 (first day of surveys considered in the analysis), as an indirect measure of water level (Seijas 1998, Seijas & Chávez 2000).

The spatial variation in abundance was analyzed comparing the obtained PI (ind/Km) between sectors of the river, and also between different sections of each sector. The comparisons were carried out using a Kruskal-Wallis test. The average values of PI of every studied section of the river were used to calculate the minimum size of the crocodile population. We estimated the density of crocodiles in unsurveyed sections of the river as a value intermediate of its immediate upper and lower sections for which information was available.

The population structure of crocodiles for the entire river, and for every sector was calculated using the maximum number of individuals in a particular size category, regardless of the survey in which they were observed, as minimum number of individuals corresponding to that category. This method is referred to by Messel et al. (1981) as the maximum-minimum (MM) method. Comparison of the population structure among river sections were made using contingency tables (\(\chi^2\)). On the other hand, monthly data of population structure were used for comparison between three hydrological periods (falling water, low water and rising water levels) according with fluctuations of the Capanaparo River during the study period. This comparison was carried out again using contingency tables (\(\chi^2\)).
RESULTS

Population indices

From October 2000 to June 2001, 44 nocturnal spotlights surveys were conducted in the three defined sectors (eight sections) of the Capanaparo River. Between five to seven repetitions (one per month) were made for every section. Results obtained during October were not considered for further analysis, because survey methodology was standardized during that month. The study area was not surveyed from July until September. During those months the high water period occurs, and the surveys would have been hindered due to the dispersion experienced by crocodilians populations. Additionally, the plains surrounding the river were flooded and the access to many places was difficult.

The lowest index of relative population abundance (PI) of crocodiles were found in Piedra Azul sector, P2 section with a value of 0.37 ind/km in February, and P3 section with a value of 0.39 ind/km in May. In contrast, higher PI values were recorded in Naure sector (N3 section during May) and Las Campanas sector (C1 section during June) with values of 2.92 ind/km and 2.73 ind/km respectively.

Although the fraction of the crocodile population that was seen during surveys showed a slight tendency to increase as the dry season advanced, the PI values were nearly constant during all the fieldwork. A correlation analysis among the fraction of crocodiles sighted and days after November 21 (established as first day of surveys) indicates that this positive relationship was not statistically significant (r = 0.21, P = 0.16).

Different months of working were grouped in three hydrological periods according with fluctuations on water level: falling waters (from November to February), low waters (March and April) and raising waters (May and June). Kruskal-Wallis test suggested that no one of the three sectors showed statistical differences related to crocodile abundance among these periods.

To analyze the spatial variation on crocodile abundance, a Kruskal-Wallis test was performed comparing the PI of each sector. Highly statistical differences resulted from the comparison of Naure and Las Campanas sectors related to Piedra Azul sector (H = 29.80, P < 0.01). The same test was performed considering every section of each sector. In this sense, we observed three groups of PI values with highly statistical differences (H = 38.30, P < 0.01). The first group (low PI values) was composed by the three sections of Piedra Azul Sector (P1, P2 and P3); the second group (intermediate PI values) was integrated by N1 section of Naure sector, and C2 section of Las Campanas sector. Finally, the third group (high PI values) was composed by N2 and N3 sections of Naure sector, and C1 section of Las Campanas sector.

The minimum population size of non-hatchling crocodiles in the entire study area was estimated to be 332 individuals (Table 1). The estimation was made using the medium PI values of every section. This is a conservative calculation because it is based on PI that was below the maximum obtained for all river sections. If the maximum PIs had been used, the estimated population would be 382 non-hatchling individuals, a 13.1% increase.

This estimation includes the portion of Capanaparo River from the confluence of Riecito River to the outlet of Capanaparo in the Orinoco River. Nevertheless, if we consider the same approach used by Thorbjarnarson (1988), to estimate the crocodile population in all the Capanaparo basin it would be necessary to consider: 1) the river portion that flows by Venezuelan territory from the Colombian border to the outlet of Riecito river into the Capanaparo, 2) the Riecito river, 3) the floodplain lagoons of Capanaparo river, and 4) other tributaries of Capanaparo river. If we assign to the high potion of Capanaparo River (from the Colombian border to the confluence of Riecito River) the lowest PI value of all surveys (0.37 ind/km), a total of 70 non-hatchling crocodiles could be estimated in that portion of river (Thorbjarnarson 1988, estimated 76). On the other hand, Thorbjarnarson (1988) estimated 71 individuals in Riecito River, 23 individuals in lagoons (oxbow and old meanders of Capanaparo River), 40 individuals belonging to other tributaries of Capanaparo River (Naure, Casanarito and La Pica streams). If these values are added to the results of our study, we could estimate that the entire non-hatchling crocodile population of the Capanaparo basin has at least 536 individuals.
Table 1. Estimated number of non-hatchling Orinoco crocodiles in different sections of Capanaparo River.

<table>
<thead>
<tr>
<th>SECTION</th>
<th>Length (km)</th>
<th>Mean density (ind/km)</th>
<th>Estimated number</th>
<th>Maximum density (ind/km)</th>
<th>Estimated number</th>
</tr>
</thead>
<tbody>
<tr>
<td>La Pica – Piedra Azul P1</td>
<td>54.2</td>
<td>0.19</td>
<td>10</td>
<td>0.19</td>
<td>10</td>
</tr>
<tr>
<td>Piedra Azul P1</td>
<td>18.2</td>
<td>0.55</td>
<td>8</td>
<td>0.87</td>
<td>13</td>
</tr>
<tr>
<td>Piedra Azul P2</td>
<td>15.2</td>
<td>0.90</td>
<td>14</td>
<td>1.18</td>
<td>18</td>
</tr>
<tr>
<td>Piedra Azul P3</td>
<td>15.9</td>
<td>0.56</td>
<td>9</td>
<td>0.82</td>
<td>13</td>
</tr>
<tr>
<td>Piedra Azul P3 – Naure N1</td>
<td>40.6</td>
<td>0.37</td>
<td>15</td>
<td>0.37</td>
<td>15</td>
</tr>
<tr>
<td>Naure N1</td>
<td>15.5</td>
<td>1.41</td>
<td>22</td>
<td>1.68</td>
<td>26</td>
</tr>
<tr>
<td>Naure N2</td>
<td>14.1</td>
<td>2.18</td>
<td>31</td>
<td>2.54</td>
<td>36</td>
</tr>
<tr>
<td>Naure N3</td>
<td>11.9</td>
<td>2.11</td>
<td>25</td>
<td>2.92</td>
<td>35</td>
</tr>
<tr>
<td>San Luis – Caño Amarillo</td>
<td>32.6</td>
<td>3.09</td>
<td>101</td>
<td>3.09</td>
<td>101</td>
</tr>
<tr>
<td>Las Campanas C1</td>
<td>14.2</td>
<td>3.19</td>
<td>31</td>
<td>2.93</td>
<td>39</td>
</tr>
<tr>
<td>Las Campanas C2</td>
<td>47.0</td>
<td>1.40</td>
<td>66</td>
<td>1.61</td>
<td>76</td>
</tr>
<tr>
<td>TOTAL</td>
<td>279.4</td>
<td></td>
<td>332</td>
<td></td>
<td>382</td>
</tr>
</tbody>
</table>

a Just one 15 km survey was carried out during November of 2000.

b Not surveyed. Assigned the minimum density of all surveys

c Just one 6.15 km survey was carried out during May of 2001.

Population structure

In Piedra Azul sector the population was composed by a major proportion of Class II individuals (38.24%), followed by Classes V, III and IV (29.41%, 23.53% and 8.82% respectively). In Naure sector we also observed a major proportion of Class II crocodiles (35.8%) followed by Classes III and IV (22.22% each one) and finally Class V (19.75%). In Las Campanas sector, in contrast, a major proportion of adult crocodiles was observed (30.61% of Class V individuals), followed by Class II (28.57%), III (24.49%) and IV (16.33%) (Figure 2).

The differences between sectors structure were not statistically significant ($\chi^2 = 5.026$, P = 0.54). The same comparison was carried out grouping crocodiles in categories (juveniles, sub-adult and adult), however this new frequency distribution used in the analysis, no statistical differences were obtained ($\chi^2 = 4.55$, P = 0.33).

![Population structure of Orinoco crocodile population in different sectors of Capanaparo River. Size-Class categories are expressed in cm of total length.](image)

DISCUSSION

Godshalk (1978, 1982) highlighted the Capanaparo River as one of the places were could be found a relatively important population of Crocodylus intermedius in Venezuela. This was confirmed later by the works carried out by Thorbjarnarson (1988), and Thorbjarnarson & Hernández (1992). We found an Orinoco crocodile population with a minimum size of 332 non-hatchling individuals, from the outlet of Riecito river to the confluence of Capanaparo in the Orinoco river. This value is notably higher than the 233 non-hatchling
individuals reported by Thorbjarnarson (1988) for the same segment of Capanaparo river. On the other hand, at least 40% of the crocodile population is composed by sub-adult and adult individuals, situation which also overcomes the estimation of 100 individuals longer than 150 cm (TL) made by Thorbjarnarson & Hernández (1992). These differences could principally due to two factors:

1. The survey methodology used. The anterior authors based their results for the major portion of the river in airplane censuses, and made night surveys just in one 25 km section of river (between Caño Amarillo and San Luis community).
2. The fact that between 1991 and 1993, 571 individuals were released in Capanaparo River (Arteaga et al. 1997).

Even though is difficult to make an exact comparison between Thorbjarnarson (1988) and Thorbjarnarson & Hernández (1992) and our results, because both studies considered sections with differences in length, we estimate that in Naure sector exist at least 60 more non-hatchling crocodiles in relation to anterior researches. This increase (25.75%) in the crocodile population size, could be due to a several release activities carried out in anterior years (all made in zones near or within Naure sector). This could be a measure of the successful of that release program for the recuperation (slowly yet) of the crocodile population in Capanaparo river.

It is necessary to consider that is very difficult to estimate the real size of a population. Besides, the monitoring of crocodiles presents some problems which have been analyzed by several authors (Woodward & Marion 1978, Messel et al. 1981, Magnusson 1982, Larriera et al. 1993, Abercrombie & Verdade 1995, Pacheco 1994, Pacheco 1996). It is theoretically possible to control the effect that most of the environmental variables have over night surveys always carrying out them under similar conditions, but it is more difficult to control biological variables as wariness and population density (Pacheco 1994, 1996). In areas where animal hunting with different porpoises has been (or still is) a common practice, crocodiles tend to be more shy, that which can hinder their observation and to produce a bias when calculating the abundance. The tendency to sub-estimate the real population size is present to in populations with very low abundance index or low density, since it diminishes significantly the probability to observe an individual. Finally, the relative abundance indices are going to sub-estimate the real size of that population because a part of this is remains usually undetected, and is too difficult to establish the relationship between abundance index and the real density of the population in the zone (Hutton & Woolhouse 1989).

The environmental factor that could have more effect over night counts of crocodilians is the water level (Woodward & Marion 1978, Messel et al. 1981, Llobet & Goitia 1997). However, this variable can be related with behavioral changes which could affect also the results of surveys. Seijas & Chávez (2000) in Cojedas River System reported variations in the number of crocodiles observed as the dry season occurred; on the other hand, this same authors observed an increase of adult crocodiles (most of them females) at the beginning of the reproductive season. In the present study there were no significant variations in the number of crocodiles sighted as the dry season lapsed, probably because the particular conditions of Capanaparo river, where all the crocodiles (widespread in a large area) count with many basking zones from November to June; this situation could reduce the intra-specific competition, so juvenile animals are not forced to seek for refuges.

Other factors that may explain the variability in abundance index (PI) are related with differences in visibility among sectors, which could introduce some bias in the results (Hutton & Woolhouse 1989, Da Silveira et al. 1997). The Capanaparo river, besides having extended sand beaches, shows step banks many times covered with riparian vegetation, which could serve to crocodilians as a refuge avoiding them detection during night surveys. Differences in visibility of crocodiles in relation to water level have important implications for monitoring of population status (Seijas & Chávez 2000). According to Seijas (1998), the best period to conduct surveys to determine population size is from November to January, when a major proportion of crocodiles can be sighted, and the number of spectacled caimans (Caiman crocodilus) is relatively low, which reduces survey time, therefore, limiting observer fatigue (Thorbjarnarson & Hernández 1992). In Capanaparo River, the monthly variation of the number of crocodiles was no significant, alternatively, the number of spectacled caimans sighted increased from month to month, which had an effect in the survey effort.

The Orinoco crocodile population in the Capanaparo River is not uniformly distributed. Highest densities were observed in N2 and N3 sections of Naure sector, C1 section of Las Campanas sector, and the section between San Luis and Caño Amarillo (surveyed just once during all the study). The access to the river into these
sections is more difficult because the “sabana” roads only can be used during dry season. On the other hand, human communities are widespread and are not too much populated. The crocodile density in Piedra Azul sector (were lowest values were registered) could be affected by a bigger human pressure due to the easy access to this part of the river. These results in general agree with those reported by Thorbjarnarson (1988) and Thorbjarnarson & Hernández (1992) who reported major crocodile densities in river sections between Naure and Las Campanas sectors.

Population structure showed no statistical differences among river sectors, even though Piedra Azul and Naure sectors had a major proportion of juvenile crocodiles, and Las Campanas sector showed a population structure dominated by adult crocodiles. Population structures dominated by juvenile size-classes could suggest that the population may be recovering from overexploitation (Webb & Messel 1978, Seijas 1986). However, we also must considerate that this kind of structures could due to actual human pressure exerted over adult crocodiles of the population.

The population structure could be shaped by human activities present in a zone (Seijas & Chávez 2000). Large crocodiles are more conspicuous and probably more frequently killed by people than small crocodiles. This situation, besides bad perception that local people have over crocodiles, could affect the population structure of the Orinoco crocodile in the Capanaparo River. Under these circumstances, few adult crocodile could remain in the river; meanwhile less conspicuous juveniles could escape from detection. If we consider, on the other hand, that there is a relationship between crocodiles wariness and human pressure (Pacheco 1996), we could expect to register larger escape distances in zones with major human pressure. In this sense, large crocodile individuals, and probably more experienced about activities directed to its hunting or capture, will be more shy than juveniles, so a new bias could be introduced over the population structure results. In those sectors with some access troubles (as Las Campanas sector), larger crocodiles could have more chances to survive, and also would behave less shy or cautious in the presence of an observer.

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LITERATURE CITED


Reproductive Status and Nesting Ecology of the Orinoco Crocodile (Crocodylus intermediaid) in the Cojedes River System, Venezuela

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ABSTRACT: During 1996-1997, ninety-one reproductively active Orinoco crocodiles (males and females) were estimated for the Cojedes River System (CRS), Venezuela. In those years at least 48 different female crocodiles nested in 45.7 km of surveyed sections of the CRS. The reproductive population was mostly found in Caño de Agua (63.2%) and in the lower Sarare River, areas with the best quality nesting habitat. Egg-laying starts during the months of lowest precipitation (January-February) and hatching takes place at the onset of the rainy season (late April-early May). The average number of hatchlings per pod was 26.0±13.9. The distribution of nests along the rivers suggests a polygynous system, in which dominant males form groups with two or more females. Lack or scarcity of good nesting substrate seems to be an important factor determining the current distribution of the species in the CRS. Most frequently selected nesting sites are composed of a high proportion of sand (>70%). There are no evidences that the species toward the south end of Cojedes and in La Culebra, river sections with relatively poor nesting habitat. Several km of good nesting habitat have been lost since 1991 due to river diversion. Data collected from 1998 to 2002 indicated a high variability in hatching success, presumably related to changes in the level of river at the end of the incubation period.

Keywords: Orinoco crocodile, Crocodylus intermedius, reproduction, nesting habitat.

RESUMEN: Durante 1996-1997 se estimó en 91 el número de cocodrilos del Orinoco reproductivamente activos (machos y hembras) en el sistema del río Cojedes (SRC), Venezuela. En esos años al menos 48 hembras de cocodrilos anidaron en 45.7 km muestreados del SRC. La población reproductiva se concentra en Caño de Agua (63.2%) y en la sección baja del río Sarare, áreas con los mejores hábitat de anidación. La postura de huevos comienza en los meses de precipitación más baja (enero-febrero) y la eclosión ocurre al comienzo de la estación lluviosa (finales de abril- comienzos de mayo). El número promedio de crías nacidas por nidada fue 26.0±13.9. La distribución de nidos a lo largo de los ríos sugiere un sistema polígamio, en el cual un macho dominante se agrupa con dos o más hembras. La falta o escasez de buen sustrato de anidación parece ser un factor importante en la determinación de la distribución actual de la especie en el SRC. Los lugares de anidación más frecuentemente utilizados están compuestos de una gran proporción (>70%) de arena. No hay evidencia de que la especie se reproduzca en la sección sur del Cojedes y en Caño La Culebra, secciones con baja calidad de hábitat de anidación. Varios km de buen hábitat de anidación se han perdido desde 1991 debido al desvío del río. Datos colectados entre 1998 y 2002 indican una gran variabilidad en el éxito de eclosión, presumiblemente debido a cambios en el nivel del río en la etapa final del periodo de incubación.

Palabras claves: Cocodrilo del Orinoco, Crocodylus intermedius, reproducción, hábitat de anidación.

INTRODUCTION

Little have been published on the reproductive ecology of the Orinoco crocodile (Crocodylus intermedius), one of the most critically endangered crocoidilian species of the world (Ross, 1998). Basic information on this regard was published by Medem (1981, 1983). Thorbjarnarson and Hernández (1993a, b), working both with captive and wild crocodiles, shed some light on several aspects of the reproductive ecology of the species.

The largest populations of the Orinoco crocodile is found in the Cojedes River system (CRS), at the periphery of the Orinoco crocodile distribution (Seijas and Chávez, 2000). Ayarzagüena (1987) and González-
Fernández (1995) reported data on the reproductive status and ecology of the Orinoco crocodile in the CRS, an area currently under heavy anthropogenic pressure due to its proximity to some of the important agricultural, urban and industrial centers in the country (Godshalk, 1978, 1982; Ayarzagüena, 1987, 1990; Seijas, 1998). In the last 40 years, human activities have changed the characteristics of the Orinoco crocodile habitat in the CRS. Some changes have modified the water quality of the river. Others have altered the physical characteristics of the river through damming, dredging, and canalization (Seijas, 1998). To what extent have these alterations affected reproduction of the Orinoco crocodile? It has been suggested (Ayarzagüena, 1987) that dredging and canalization, for example, have a negative impact on crocodiles because it destroys nesting beaches. This should translate into a reduced nest density in modified sections in comparisons to sections where the river maintains its meanders. The main objectives of this study were (1) to answer basic questions on the reproductive ecology of _C. intermedius_ in the CRS in reference to nesting chronology, nesting habitat, reproductive success, reproductive status, parental care, and (2) discuss the reproductive ecology of the species in the context of the anthropogenic modifications of the CRS.

**STUDY AREA AND METHODS**

This study was conducted in the mid and lower reaches of the Cojedes River System of north-central Venezuela (Figure 1). In the CRS rivers flow from the northeast to southeast through several types of landscapes that vary in relief, land-cover types, and main human activities. In the northern part of the CRS, agricultural lands dominate the landscape and are interspersed with large-and medium-sized urban centers and cattle ranches. The southern part of the region (south of the Lagunitas-Santa Cruz road) is a matrix of forested savannas and cattle pastures intermixed with forest relicts, scattered agricultural lands, wetlands, and other less extensive land-cover categories. The CRS has zones of relatively high human population densities in the north, where the cities of San Carlos (>80,000 people) and Acarigua (~200,000 people) are located and the rivers there have been modified by damming, canalization, dredging, contamination, and deforestation. Human population densities are lower downstream, in the south, with El Baúl (~6,000 people) as the largest town. Human impact in this part of the study area is less apparent.

![Figure 1](image1.png)

**Figure 1.** Map of the study area (Cojedes river system) Venezuela, indicating the position of landmarks, reference points, and main river reaches surveyed.
There are two clearly defined seasons in the study area. The rainy season extends from May to October, and the dry season from December to March. April and November are transitional months. The annual mean precipitation (1975-1996) is 1323 mm in the middle part of the study area and a little higher (1514 mm) toward the south at El Baúl (MARNR, 1997). During the rainy season the river discharge increases (Figure 2) and frequently overflows its banks and inundates the floodplain, particularly in the southern portion of the study area. The annual range between the absolute minimum and maximum temperatures is 11.6 °C (21.7°-33.3 °C)(MARNR, 1995).

![Figure 2. Pattern of precipitation in the Cojedes river system area of Venezuela](image)

During nocturnal spotlight surveys and daylight reconnaissance, we collected information on aspects of reproductive ecology of the Orinoco crocodile in the CRS, such as nest location, nesting and hatching chronology, and clutch size. A part of the river shore was subjectively considered as potential nesting place for *C. intermedius* if it had one or more of the following characteristics: (1) It consisted mostly of lightly compacted material and generally had excavations made by other reptilians such as iguanas (*Iguana iguana*) or turtles (*Podocnemis unifilis*), species with similar nesting requirements in terms of soil texture; (2) The shore was bare or sparsely covered by vegetation; (3) it was 1.5 m or more above the water level, and (4) there was a record of previous utilization of the place by nesting females. The number of beaches adequate for nesting of Orinoco crocodile was counted in two sections of Caño de Agua, and in the section between Merencure and Caño Amarillo opening (see Figure 1).

The soil composition of samples of the substrate from nesting beaches was determined, as was the substrate from the river bank in sections where nesting beaches (according to the preceding criteria) were not present. The proportion of silt, clay and sand in those samples was determined following the hydrometer method of Bouyoucos (Foth, 1978) at the *Universidad Nacional Experimental de los Llanos Occidentales 'Ezequiel Zamora'* (UNELLEZ) in Guanare, Venezuela.

After hatching from the nest, neonates remained in well defined groups or ‘pods’ for several weeks. During the nocturnal surveys, the location and number of pods, and the number of hatchlings in each pod were recorded. When a particular pod was counted more than once, the maximum number of hatchlings recorded was taken as the pod size. A preliminary measure of hatching success was obtained by comparing the average number of hatchlings per pod against the average number of eggs per clutch. The average clutch size was calculated combining our own data with information found in the literature. Due to predation and dispersion of hatchlings, pod size decreases with time and only those pods found in April or early May were considered in the analyses.
The presence or absence of an adult crocodile in the proximity of the pod was recorded and taken as an indication of parental care. A contingency table analysis was used to establish if parental care of hatchling pods differed between river sections under different human pressure.

The nesting chronology of the species was determined based on reports of Ayarzagüena (1987) and González-Fernández (1995) and our own observations on dates of nest construction, banding of eggs, hatching period, sizes of the hatchlings, and size of the umbilicus of the hatchlings.

During 1996 and 1997, the position of each nest (or pod of hatchlings) was recorded with a Global Positioning System (Magellan 4000 and 4000xl). We assumed that females tend to nest in the same spot year after year, a behavior that is well documented for many crocodilian species (Garrick and Lang, 1977; Ogden, 1978; Thorbjarnarson and Hernández, 1993a). The minimum number of nesting females in the survey area was determined by comparing the relative position of nests and pods from 1996 and 1997.

The size of the reproductive population was estimated based on the number of nesting females. The number of dominant males was calculated as one per female for relatively isolated females, and up to one male for every four females for localities with several females, depending on the relative proximity of the nests. The last estimate is conservative if we take into account that the sex ratio reported by Thorbjarnarson and Hernández (1993b) is 1:2.2. In non-surveyed sections of the CRS the number of nesting females was subjectively estimated based on the characteristics of the section and the known nest densities in contiguous upper and/or lower reaches of the river.

RESULTS

Nesting Habitat

Three river segments were examined for the presence of potential nesting habitat (Table 1): (1) A 4.7 km section of Caño de Agua south of Puente Nuevo (PN). There, the river was very narrow (8-12 m) and has numerous meanders despite having been dredged an unknown number of times in the past. Both margins of the river have been deforested and grasses and bushes cover the banks down to the water's edge. Most of this part of the river (60%) was lost during the rainy season of 1996 (see below). (2) Caño de Agua Sur (CAS) is also very narrow (in general less than 12 m) and it is the most meandering river segment of the entire study area. Most of the banks were forested and grasses were less abundant than in the PN section and usually did not reach the water's edge. Scattered groups of logs and branches of fallen trees were found along the river. Dense clumps of the riparian shrub (*Alchornea castaneifolia*) also were frequently found along the river edge. (3) The part of the Cojedes river from Mercure to Caño Amarillo opening (CAM), where the Cojedes River was relatively wide (15-20 m) with ample meanders and with the banks covered mostly by forest. The shrub *A. castaneifolia* was very common in this part of the river. Most of the beaches counted along this section were found approximately in the first 4 km downstream from Mercure. In the remaining downstream part of this river section appropriate beaches were almost nonexistent; grasses and *Heliconia* plants were abundant and reach the water’s edge.

**Table 1.** Number of beaches considered as potential nesting habitat in three river reaches in the Cojedes River system

<table>
<thead>
<tr>
<th>Place</th>
<th>Length (km)</th>
<th>Number of beaches</th>
<th>Beaches per kilometer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caño de Agua, downstream from Puente Nuevo (PN)</td>
<td>4.7</td>
<td>16</td>
<td>3.40</td>
</tr>
<tr>
<td>Caño de Agua Sur (CAS)</td>
<td>5.2</td>
<td>20</td>
<td>3.85</td>
</tr>
<tr>
<td>Mercure-Caño Amarillo (CAM)</td>
<td>8.4</td>
<td>9</td>
<td>1.07</td>
</tr>
</tbody>
</table>

In the sections of the river that had been canalized, river banks that fulfill the criteria as potential nesting beaches were scarce or absent. Caño de Agua Norte (CAN), upstream from Puente Nuevo, has been dredged and partially canalized over the last 20 years but in some parts it has recovered its meandering condition. In those latter reaches the characteristics of the river were the same as downstream from the bridge, but in the river
segments that remained canalized, banks were very steep and nesting beaches were absent. In the southern part of the study area near Sucre (SUC) and at Caño La Culebra (CUL) adequate nesting habitat was also scarce.

In early February 1997, a small number of beaches (15) from CAS and CAM were more carefully scrutinized to determine their use by iguanas and turtles. Twenty percent of the beaches had clutches of turtles’ eggs (*Podocnemis unifilis*). Most of these beaches (73.3%) also had nest excavation made by iguanas. The count for turtle nests was clearly an underestimation, because it is much more difficult to find turtle clutches than iguana excavations. On the other hand, it was probably too early in the nesting season of *Podocnemis* and many turtles may not have nested yet. González-Fernández (1995) found turtle nests in 38% of the beaches with crocodile nests. In a nocturnal survey conducted from La Batea to Merecure on 27 April 1997, the remains of eight turtle nests were found. Turtles or turtle nests have never been observed in the northern part of the study area at CAN and Cojedes Norte (CON).

In SUC, turtles were seen frequently basking on logs or branches of fallen trees. They may nest in that area, although nesting was never observed. Iguanas were very rare in this part of the river, which had its banks profusely covered by trees. This suggests that iguanas may be limited by scarcity of nesting substrate. Adequate nesting substrate in CUL seemed to be also scarce, but the presence of iguanas cannot be used there as an indicator of quality of nesting habitat, because that part of the CRS is almost devoid of arboreal vegetation, which may signify a more important limiting factor for iguanas.

Another criterion for evaluating the suitability of a section of the river for nesting was through the analysis of soil texture. Samples from the northern sections of the study area showed a preponderance of sand in their composition (65.5-89.5%; Figure 3). In two samples from CAS, close to Merecure, sand accounted for 58.5% on average. A lower percentage of sand was found in La Culebra (54.8%), and the lowest percentages of sand in all the samples were obtained in Sucre (range 11.5 to 23.5%).

![Figure 3](image_url)

**Figure 3.** Texture of river bank soil samples collected at different locations along the Cojedes river system, Venezuela. Locations are ordered from north to south (top to bottom).

Although vast parts of the study area were not evaluated for their suitability for nesting, a pattern of decrease in the quality of the substrate on the banks from north to south was apparent.

**Nest density and nesting success**

Based on the comparisons of the positions of nests and pods from 1996 and 1997, we estimated that there were at least 48 nesting females in the surveyed sections of the study area. Those sections represent a total of...
45.7 km of river with a density of 1.03 nests (or nesting females) per km (Table 2). Although Cojedas Norte was never surveyed during the time when hatching occurs (late April early May), the size of many of the crocodiles seen there indicated that successful reproduction has taken place in that part of the river in previous years. CON is isolated from the rest of the study area by a dam. That dam constitutes a barrier that effectively blocks passage from downstream.

Table 2. Number of Orinoco crocodile females that nested in several river sections of the Cojedas river system during 1996 and 1997.

<table>
<thead>
<tr>
<th>River section</th>
<th>Length (km)</th>
<th>Nesting Females</th>
<th>Density (female/km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caño de Agua Norte (CAN)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Retajao</td>
<td>--</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td>Doncella-Guamita</td>
<td>5.5</td>
<td>4</td>
<td>0.73</td>
</tr>
<tr>
<td>Guamita-Puente Nuevo</td>
<td>10.5</td>
<td>12</td>
<td>1.14</td>
</tr>
<tr>
<td>Caño de Agua Sur (CAS)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puente Nuevo-Carama</td>
<td>4.7</td>
<td>8</td>
<td>1.70</td>
</tr>
<tr>
<td>Pte Lorenzo-Confluence</td>
<td>7.6</td>
<td>12</td>
<td>1.58</td>
</tr>
<tr>
<td>Mereducue-Caño Amarillo (CAM)</td>
<td>9.0</td>
<td>4</td>
<td>0.44</td>
</tr>
<tr>
<td>Sarare (SAR)</td>
<td>8.4</td>
<td>7</td>
<td>0.83</td>
</tr>
<tr>
<td>Total</td>
<td>45.7</td>
<td>48</td>
<td>1.03</td>
</tr>
</tbody>
</table>

1 The nest from Retajao was a casual observation in a non-surveyed section. It was not considered for the calculation of density.  
2 Most part of this river section disappeared during the 1996 flooding

Nesting females were not uniformly distributed along the river. In the river section La Doncella-Guamita only four nest (0.73 nest/km) were observed. This river reach was completely canalized and had steep banks. Downstream from it, in the Guamita-Puente Nuevo section of Caño de Agua, the river had recovered its meandering conditions. Nest density there increased to 1.14 per km.

The highest density (1.7 nesting females/km) was found in 1996 in the 4.7-km of Caño de Agua south of Puente Nuevo. Most of that the river section (approximately 60% ) was lost during the rainy season of 1996 due to river diversion after a severe flooding event, when the river changed its course and diverted into smaller branches toward Caño Camoruco. The fate of the 8 nesting females from that part of the river is not known. Two nests found near Puente Nuevo in 1997, just north of the diverted river section, might have belonged to some of these females.

Four km of CAS, between Camoruco mouth and Puente Lorenzo (Figure 4), were not surveyed for nest or hatchlings. Considering that the characteristics of that river section were very similar to the ones found immediately downstream, in the section Puente Lorenzo-Confluence, six

![Figure 4](image-url) Orinoco crocodile nests found during 1996 and 1997 in the Cojedas river system, Venezuela. Nests tend to occur in clusters, indicating the presence of a dominant male a one or more females.
additional nesting females, not listed in Table 2, could be expected in Caño de Agua Sur.

In the Sarare River, only a stretch of 8.4 km (SAR) was surveyed for nest or pods, resulting in a density of 0.83 nest/km. The river section from there down to the confluence with Caño de Agua has never been surveyed.

No hatchling or nest was ever found in Sucre or Caño La Culebra. The size of the crocodiles seen or captured there indicates that they were older than a year, suggesting that crocodiles in these locations may have come from elsewhere, probably upstream.

A detailed examination of crocodile nest distribution revealed a pattern of clustering (Figure 4). Groups of up to four females were found in close proximity, suggesting the presence of a dominant male and a group of females, as has been reported in the Capanaparo River by Thorbjarnarson and Hernández (1993b).

Nest predation by humans did not seem to be an important factor affecting the viability of the Orinoco crocodile in the CRS. One nest seemed to have been taken by people in the section Merecure-Caño Amarillo in 1997, but the evidence was equivocal. People in Retajao took at least 11 hatchlings from a pod in 1996.

Since 1994, reproductive success in the CRS has been monitored repeatedly (but only partially due to logistic problems) along the lower part of Caño de Agua Sur and the Cojedes River from its confluence with the Sarare river and Caño Amarillo, a continuous section of about 20 km. The results (Table 3) indicate a high variability in hatching success, probably related to changes in water levels at the end of the incubation period (late April).

Table 3. Number of nests of Orinoco crocodile that produced hatchlings in lower Caño de Agua Sur and Cojedes between Camoruco and Caño Amarillo. Data for 1994 was taken from González-Fernández (1995); data for 1998 and 1999 were taken from Chávez (2000).

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of successful nests</th>
<th>River length surveyed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>21</td>
<td>17.6</td>
</tr>
<tr>
<td>1996</td>
<td>5</td>
<td>17.6</td>
</tr>
<tr>
<td>1997</td>
<td>7</td>
<td>13.6</td>
</tr>
<tr>
<td>1998</td>
<td>16</td>
<td>13.6</td>
</tr>
<tr>
<td>1999</td>
<td>16</td>
<td>13.6</td>
</tr>
<tr>
<td>2000</td>
<td>13</td>
<td>4.0</td>
</tr>
<tr>
<td>2001</td>
<td>9</td>
<td>13.4</td>
</tr>
<tr>
<td>2002</td>
<td>0</td>
<td>18.0</td>
</tr>
</tbody>
</table>

Adult Population

Ninety-one reproductively active crocodiles were estimated for the Cojedes River System, most of them (63.2%) in Caño de Agua (Table 4). This figure represents a minimum since (1) some parts of the river were poorly surveyed and, conservatively, a low density of adults was assigned to them, and (2) not all the adult females nest every year.

Table 4. Reproductive population of Orinoco crocodiles in the Cojedes River System. The number of dominant males was calculated as one per female for relative isolated females, and one male for every three-four females for places with several females.

<table>
<thead>
<tr>
<th>Place</th>
<th>Length (km)</th>
<th>Nesting Females</th>
<th>Dominant Males</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cojedes Norte (CON)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caño de Agua Norte (CAN)</td>
<td>7</td>
<td>21</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Toma Cojedes-La Doncella</td>
<td>25.5</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Doncella-Guamita</td>
<td>5.5</td>
<td>4</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Guamita-Puente Nuevo</td>
<td>10.5</td>
<td>12</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Caño de Agua Sur (CAS)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puente Nuevo-Carama²</td>
<td>4.7</td>
<td>8</td>
<td>3</td>
<td>11</td>
</tr>
</tbody>
</table>

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Hatchling Pods and Parental Care

Based on the size 44 pods observed in the first month of the hatching season (Figure 5), the average number of hatchlings per pod was 26.0 °13.9, as compared to 31 °10 reported by González-Fernández (1995). When analyzing for the differences in pod size among localities (CAN, CAS+CAM, and SAR), the statistical result was significant (Kruskal-Wallis Test; X=6.2, P=0.045). This result is a consequence of the higher number of individuals (35.5) in pods from the Sarare River. Pod size in CAN and CAS+CAM was very similar (24.0 and 22.1 hatchlings/pod, respectively).

According to my own data, and on information reported by Ayarzagüena (1987) and González-Fernández (1995), the average number of eggs per clutch in the CRS is 38.2 °11.0 (n=12), which is below the typical range (40-70) mentioned for the species by Thorbjarnarson (1992). The mean pod size found in this study (26.0) represents 68% of the average clutch size, which could be taken as a preliminary measure of hatching success. A flaw in this method of calculating hatching success is that nests that fail to produce hatchlings could not be detected, and so are not included in the calculations. There is no information on other wild Orinoco crocodile populations to compare these results.

Figure 5. Frequency distribution of pods of Orinoco crocodile hatchlings according to their number of individuals in the Cojedes river system, Venezuela. Large pods may result from the integration of hatchlings from more than one female.

<table>
<thead>
<tr>
<th>Place</th>
<th>Length (km)</th>
<th>Nesting Females</th>
<th>Dominant Males</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Camoruco-Pte. Lorenzo</td>
<td>3.7</td>
<td>61</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Pte Lorenzo-Confluence</td>
<td>7.6</td>
<td>12</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Confluence-Caño Amarillo</td>
<td>9</td>
<td>4</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Caño Amarillo-Sucre</td>
<td>51</td>
<td>11</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Caño Amarillo-La Culebra</td>
<td>33.5</td>
<td>11</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Sarare Downstream Amparo bridge</td>
<td>8.4</td>
<td>7</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Lower Sarare</td>
<td>12</td>
<td>81</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>153</strong></td>
<td><strong>66</strong></td>
<td><strong>25</strong></td>
<td><strong>91</strong></td>
</tr>
</tbody>
</table>

1 Not surveyed. Figure estimated based on similarity of appearance with surveyed sections.
2 Most of this river reach disappeared during the flooding season of 1996.

Nesting Chronology

The earliest observation of hatchlings crocodiles was 12 April, during the 1996 hatching season. Morphological characteristics (total length, presence of egg tooth and size of the umbilicus) of the hatchlings found in 72 pods observed from 1991 to 1997, suggest that most of the hatching occurred from mid-April to early-May. In captivity, under ideal conditions, the incubation period lasts some 80-85 days (Ramo et al., 1992; Thorbjarnarson and Hernández, 1993a; Seijas and González, 1994; Lugo, 1995), so construction of nests may start as early as mid January. Most nesting, however, occurs in late January and early February. The earliest nest ever examined by us, on 5 February 1997, and those found by Ayarzagüena (1987) support this conclusion.
In 47.7% of 44 pods for which the information was recorded, an adult crocodile, presumably the mother of the hatchlings, was seen in close proximity. This figure is surely an underestimation, because the disturbance produced by the noisy approach by boat, powered by an outboard engine, might have caused many females to disappear from sight. Compared to CAN, the river sections of CAS and CAM are less disturbed by human activities (Seijas, 1998, 2001). We expected that human disturbance affect pod attendance. The differences in pod attendance was lower in CAN, supporting that hypothesis (X²=4.48; P=0.034).

**DISCUSSION**

Although depleted in most of its former range, there is high density of Orinoco crocodiles in the CRS. There were at least 48 adult females in the surveyed sections of the river, a number that is most probably an underestimation since a relatively small part of the region was properly surveyed.

Lack or scarcity of good nesting substrate seems to be an important factor determining the current distribution of the species in the CRS. Soil samples taken from active nests indicates that the most frequently selected nesting sites are composed of high proportion of sand (generally more than 70%). The reproductive population is concentrated in the Caño de Agua and in the lower Sarare River, the areas that had the highest quality nesting habitat. There was no evidence that the species reproduces in Cojedes Sur and in Caño Culebra, areas which had lower quality nesting habitat. The abundances of crocodiles and quality of nesting sites of many sections of the CRS have not been evaluated, so this conclusion is preliminary.

Reproductive data from this study, compared to data in the literature (Ayarzagüena, 1987, González-Fernández, 1995), suggest that the number of nesting females has remained stable over the last 10 years. Globally, the total density of nests was the same as found by González-Fernández (1995) in part of the study area (1.04 nest/km). Ayarzagüena (1987) estimated that there were some 25 nesting females in Caño de Agua Sur, which was roughly the same number found in this study for the same part of the CRS. The nest density of the *C. intermedius* population in the Capanaparo River studied by Thorbjarnarson and Hernández (1993a) ranged from 0.24 to 0.36 nests/km.

Nest density in the CAM (0.44 nest/km) was relatively low when compared with the 1.4 nests/km obtained in 1994 by González-Fernández (1995). The results obtained by González-Fernández may be exceptional, because that year the rainy season started late, with the lowest combined precipitation for April-May (129.7 mm) for the period 1975-1996 (MARNR, 1997). Compared to other years, a lower number of nests (if any) may have been lost in 1994 due to flooding.

Some river sections that have been dredged repeatedly in the last 20 years had relatively high density of nesting. Dredging may have an immediate negative impact because it destroys nesting beaches (González-Fernández, 1995) but the river seems to recover after several years. One of the lowest nest densities was found in La Doncella-Guamita, a stretch that has been channelized. Channelization may have a greater impact on reproduction and on the population as a whole because it reduces the habitat for the species, eliminates most beaches, and increases the flow speed of the river, which may have a negative impact on pod cohesion and hatching survival.

The distribution of nests or nesting females along the river indicated that in the Cojedes River the Orinoco crocodile showed the same social structure described for the species in the Capanaparo River, in which dominant males form polygynous groups with two or more adult females (Thorbjarnarson and Hernández, 1993b).

If pollution and other human related factors affect egg viability in the area studied, that may be reflected in the average pod size. Habitat modification and pollution (Seijas, 1998) were higher in CAN than in CAS. Habitat alteration in the surveyed portion of the Sarare River was comparable to that found in CAN, but information on pollution was not available. There was a statistical difference in pod size among localities, due to the relatively higher average pod size in the Sarare River. However, this latter site was insufficiently sampled. Since there are many factors that can affect pod size, including female size and hatching success, it is difficult to interpret the meaning of these differences in pod size. More detailed studies in this regard are necessary, particularly on the effects of contamination on crocodile reproduction.
There was a significant difference in what was interpreted as maternal care or pod attendance between Caño de Agua Norte and Caño de Agua Sur-Caño Amarillo. This may be a consequence of higher human interference in Caño de Agua Norte, as has been reported for Caiman yacare in Brazil (Crawshaw, 1987). Another possibility is that females in Caño de Agua Norte were relatively new colonizers of the area and probably younger and less experienced than females in southern locations.

Egg or hatching collection did not seem to be a factor that affects the survival of the Orinoco crocodile in the CRS, at least where most of the nesting occurs, although anecdotal information indicated that this kind of human intervention occurs sporadically (pers. observ; González-Fernández, 1995) and probably was common practice in the past (Godshalk, 1978). Human settlements are generally several kilometers away from the river banks, and in the CRS is not inhabited by people exploiting the river resources as is the case in the Capanaparo River (Thorbjarnarson and Hernández, 1992). Gonzalez-Fernandez (1995) reported that 2 of 27 (7.4%) nests analyzed by him were destroyed by a dredge, but no predation by human was reported.

Nesting chronology documented in this study agrees with the general pattern described for the species (Medem, 1981, 1983; Ramo et al., 1992; Thorbjarnarson and Hernández, 1993a): egg-laying starts during the months of lowest precipitation (January-February) and hatching takes place at the onset of the rainy season (late April-early May). Nesting (and consequently hatching) occurs earlier in the captive breeding facilities of the Universidad Nacional Experimental de los Llanos (UNELLEZ), and later in the breeding facilities of Masaguara ranch, in response to different precipitation regimes in those areas (Ramo et al., 1992, Thorbjarnarson and Hernández, 1993a). Eggs laid late during the nesting season are under a high risk of being lost due to flooding. The high nesting success reported by González-Fernández (1995) for a reach of the Cojedes River (Merecure-Caño Amarillo) in 1994 may be the result of delay of flooding events in that year. The impact that damming, channelizing and water diversion in the CRS may have on nesting and reproductive success of the Orinoco crocodile has not been properly studied. Several kilometers of good nesting habitat have been lost due to flooding and river diversion in the last 10 years. The wise management of the Las Majagua reservoir and of the future Las Palmas reservoir, to avoid sudden rises of water levels and losses of nests, will be crucial for the survival of the species.

ACKNOWLEDGMENTS

This study was made possible by a grant from the Wildlife Conservation Society (WCS). Jevert González, Eddy Escalona and particularly the late Coromoto Ramírez served as our guides on many occasions. Early version of the manuscript were reviewed by F. W. King, John Thorbjarnarson, Richard Bodmer, Melvin Sunquist, George Tanner and Robert Godshalk.

LITERATURE CITED


MARNR. 1997. Datos mensuales y anuales de precipitación (mm). Estación Palo Quemado. DGSICASV, Dirección de Hidrología y Meteorología. SINAIHME. (unpublished information)


Habitat Requirements and Aggregation Patterns of Different Age Groups of Indian Gharial, *Gavialis gangeticus* (Gmelin)

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**ABSTRACT**: The systematic depletion of crocodile species in their natural habitats has led to the establishment of rehabilitation programmes in India. To assess the natural recruitment rate and breeding potential, population was monitored in the Chambal River (National Chambal Sanctuary) by observing behaviour of different age groups of Gharial (*Gavialis gangeticus*). All gharials of different age groups, starting from hatchlings to adults, are counted during annual surveys. The gharial is a gregarious species. Young gharials are congregated into small groups of 10 to 20 individuals and prefer shallow areas with sand peninsulas. The breeding adults (one male group) are living in deep pools with steep sand banks. The young gharials migrate frequently until they attain maturity. The adults remain in the breeding areas and rarely leave their breeding grounds. The hatchlings have a short period of 15 to 20 days of attachment with their parents, whereas the adults form a breeding group for many years in specific areas. Presence of age specific habitat conditions made the Chambal River an ideal habitat for the Indian Gharial. Although rehabilitation of gharial in other rivers has been carried out, the rehabilitation of gharial in the Chambal River is most successful programme under Indian Crocodile Project.
Extinct Crocodiles Had Specialized Sensory Organs to Detect Water Surface Disruptions

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ABSTRACT: Crocodilians are an ancient monophyletic group. Living crocodilians are divided into alligatorids, crocodiles and gavials. All have an amphibious life-style, spending their time on land, underwater and on the interface of the two media, although some extinct forms were strictly terrestrial or aquatic. Behavioral, anatomical and physiological data shown here demonstrate that these predatory animals have evolved a unique sensory organ that mediates orientation to disruption of the water surface. Pressure waves created by these disruptions stimulate dome pressure receptors (DPR, formally known as integumentary sensory organs) on the crocodilian skin. Removing DPRs abolishes the orienting behavior. The ancient nature of these sensory organs is reflected in the fossil record. Typical patterns of foramina in jawbones associated with DPR innervation appear in extinct specimens in the early Jurassic. These osteological markings are present only in animals believed to have had an amphibious life style and are absent in the extinct fully terrestrial or aquatic forms.

Everglades Alligator Thermoregulation: Unanswered Questions
Clarence L. Abercrombie, Stanley R. Howarter, H. Franklin Percival, Kenneth G. Rice, Cory R. Morea

ABSTRACT: We instrumented 29 free-ranging, adult Everglades alligators with intra-peritoneal data loggers that recorded time and temperature at 72-min intervals. About 1 year later we recovered functioning data loggers from 13 animals. Alligator temperature data were available from August 1997-June 1998; some environmental temperatures were recorded from October 1997- May 1998. The relationship between alligator- and environment-temperatures suggested thermal conformity during winter and fall, but alligators were warmer than most of their environment in spring. In winter, alligators did not generally seek high temperatures, and T_b’s typically conformed to deep-water temperatures—except that alligators warmed episodically to about 30°C. Although T_b’s were usually correlated across alligators, these winter spikes occurred on different days for different alligators. When alligators were clustered by thermal histories, statistically significant clusters reflected animal mass.

INTRODUCTION, MATERIAL, AND METHODS

Although ectothermic archosaurs once dominated large-vertebrate niches, crocodilians are the sole surviving members of this vast radiation. And of 23 extant crocodilians species, only American and Chinese alligators are primarily temperate in distribution. Therefore, thermoregulation in these species is particularly interesting.

In May-September, 1997, our veterinary team implanted Tidbit data loggers (Onset Corporation) and radio transmitters (AVM Instruments) into 29 alligators from Everglades National Park (ENP) and Conservation Area Three (CA, to the Park’s north). We monitored animals’ post-operative recovery and then released them at their capture sites. We also used Tidbit loggers to record environmental temperatures (1) under 20-50 cm of water (“deep H2O”), (2) under 5 cm of water (“shallow H2O”), (3) in air, under shade (“shade”), and (4) within 600
cm$^3$, air-filled copper spheroids painted flat-black (“black-body”). We synchronized all data loggers to record observations simultaneously.

During June-September, 1998, we recaptured alligators, retrieved data loggers, and released animals at their recapture sites. We downloaded loggers using Boxcar software (Onset Corporation) and exported data to SYSTAT 7.0. Then we validated logger-accuracy against mercury thermometers, subsequently excluding data from loggers that had malfunctioned. (We specify data-exclusion procedures in an Appendix.) Table 1 summarizes the data we analyzed.

**Table 1. Summary of data.**

<table>
<thead>
<tr>
<th>Inclusive Dates</th>
<th>Alligators Monitored</th>
<th>Environmental Temperatures Monitored</th>
<th>Observation Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>01OCT97-31MAY98</td>
<td>13</td>
<td>CA: deep H$_2$O</td>
<td>20/day</td>
</tr>
<tr>
<td>31MAY98-31JUL98</td>
<td>13</td>
<td>ENP: shallow H$_2$O, black body, shade</td>
<td>20/day</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Loggers considered insufficiently reliable.</td>
<td></td>
</tr>
</tbody>
</table>

**ANALYSES**

For initial analyses, we defined 10 variables (see Appendix for definitional details):
1. Average alligator temperature: $G_{ave}$ is mean temperature calculated across 12 alligators.
2. Environmental temperature index: $E = [2(\text{deep } H_2O) + \text{shallow } H_2O + \text{shade}]/4$.
3. Temperature difference, alligator – environment: $D_{ave} = G_{ave} - E$.
4. Daily temperature cycle intensity: **INTENSE** is largest component in Fourier decomposition of a time-series of alligator temperatures. (Note: this was always the daily component.)
5. Circadian response ratio: **RATIO** = INTENSE/largest Fourier component for environment temperatures. (Note: largest Fourier component for environment was also the daily component.)
6. Smoothed temperature difference, alligator - environment: $D_{smooth}$ is the weekly running median of $D_{ave}$.
7-8. Alligator maximum and minimum temperatures: $T_{max}$ is the maximum temperature of an alligator during a specified time period. $T_{min}$ is the minimum temperature of an alligator during a specified time period.
9-10. Environmental maximum and minimum temperatures: $E_{max}$ is maximum of (shade, shallow $H_2O$, deep $H_2O$); $E_{min}$ is minimum of (shade, shallow $H_2O$, deep $H_2O$).

We plotted $D_{smooth}$ as a function of date. We calculated monthly averages for D and for RATIO variables. We determined correlations, by month, between alligator $T_b$’s and black-body temperatures. Taking January as an example of winter, we compared time-series plots of each alligator’s $T_b$ against time-series plots of environmental temperature measures. We also compared pairs of alligator time-series $T_b$ plots, and we listed days on which individual alligator $T_b$’s exceeded 30°C (the value was arbitrarily selected, but see Colbert et al., 1946; Avery, 1982; Coulson and Hernandez, 1983).

For each month and each sequential pair of months we performed a joining-cluster analysis to determine which alligators might exhibit similar thermal patterns. Three clustering variables were defined: (1) mean for month(s) of daily $T_{max}$, (2) mean for month(s) of daily $T_{min}$, and (3) INTENSE. See Appendix for technical details. Because our analyses indicated that body mass was important in the thermal clustering of alligators, we investigated this hypothesis, by month, using linear regression.

**Finding # 1: Relative to their environment, alligators warm up in spring.**

Although our alligators were approximate thermal conformers throughout much of the year, in spring they apparently sought warm temperatures. This contention is supported by 3 analyses.

First, Fig. 1 plots $D_{smooth}$ for all alligators as a function of date for 1 October 1997 – 31 May 1998. Although the graph is noisy, values of $D_{smooth}$ clearly fluctuate near difference = 0 until late February, after which the alligators become substantially warmer than most of their environment.
Second, Table 2 shows monthly averages of $D_{\text{ave}}$. Note differences are larger in spring (March, April, and May) than at other times.

Table 2. Monthly and seasonal averages of $D$, the mean difference between average alligator temperature ($G_{\text{ave}}$) and environmental index ($E$). “Fall-Winter” includes January, February, and October-December, and “Spring” includes March-May.

<table>
<thead>
<tr>
<th>Month</th>
<th>$D$ (or, $G_{\text{ave}} - E$)</th>
<th>Month</th>
<th>$D$ (or, $G_{\text{ave}} - E$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>0.19°C</td>
<td>October</td>
<td>0.34°C</td>
</tr>
<tr>
<td>February</td>
<td>0.10°C</td>
<td>November</td>
<td>-0.32°C</td>
</tr>
<tr>
<td>March</td>
<td>1.16°C</td>
<td>December</td>
<td>0.39°C</td>
</tr>
<tr>
<td>April</td>
<td>1.55°C</td>
<td>Fall-Winter</td>
<td>0.15°C</td>
</tr>
<tr>
<td>May</td>
<td>2.57°C</td>
<td>Spring</td>
<td>1.75°C</td>
</tr>
</tbody>
</table>

Third, Table 3 shows values of RATIO by month. These values reflect the intensity of alligator heating and cooling, relative to environmental heating and cooling. Note that ratios are highest in spring, and particularly in March. Indeed, during spring the alligator circadian thermal cycle was more intense than that of their general environment index, $E$.

Table 3. Magnitudes of largest (daily) Fourier components for $G_{\text{ave}}$ ($G_{\text{Fourier}}$) and for environmental index ($E_{\text{Fourier}}$); ratio of $G_{\text{Fourier}}/E_{\text{Fourier}}$; ratio of alligator circadian magnitude to circadian magnitude of black-body temperatures ($G_{\text{Fourier}}/BB_{\text{Fourier}}$); all by month.

<table>
<thead>
<tr>
<th>Month</th>
<th>$G_{\text{Fourier}}$</th>
<th>$E_{\text{Fourier}}$</th>
<th>Ratio: $G_{\text{Fourier}}/E_{\text{Fourier}}$</th>
<th>Ratio: $G_{\text{Fourier}}/BB_{\text{Fourier}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>4.83</td>
<td>3.61</td>
<td>1.34</td>
<td>0.043</td>
</tr>
<tr>
<td>February</td>
<td>10.70</td>
<td>6.73</td>
<td>1.59</td>
<td>0.098</td>
</tr>
<tr>
<td>March</td>
<td>19.18</td>
<td>6.18</td>
<td>3.11</td>
<td>0.133</td>
</tr>
<tr>
<td>April</td>
<td>19.00</td>
<td>10.60</td>
<td>1.79</td>
<td>0.099</td>
</tr>
<tr>
<td>May</td>
<td>10.91</td>
<td>25.50</td>
<td>0.43</td>
<td>0.034</td>
</tr>
<tr>
<td>October</td>
<td>4.41</td>
<td>5.24</td>
<td>0.84</td>
<td>0.024</td>
</tr>
<tr>
<td>November</td>
<td>7.15</td>
<td>6.67</td>
<td>1.07</td>
<td>0.048</td>
</tr>
<tr>
<td>December</td>
<td>5.25</td>
<td>5.67</td>
<td>0.93</td>
<td>0.044</td>
</tr>
</tbody>
</table>

Finding # 2: In winter alligators often stay cooler than “necessary.”
As indicated by Fig. 1 and Table 2, average alligator temperatures were close to our environment-temperature index except during spring. However, “thermal conformity,” does not entirely describe our alligator temperatures in winter. During January the average temperature of each study-alligator was lower than the average shallow-water temperature. And, as a group, alligators averaged 3.6°C cooler than shallow H₂O in January. Presumably, alligators could have moved toward heat and averaged at least as warm as the shallow water in an Everglades-type environment, but they did not.

Finding # 3: Nevertheless, sometimes winter alligators warm appreciably, perhaps by using solar-radiant energy.

Recall that at any given time, $E_{\text{max}}$ is the maximum of shade, shallow H₂O, and deep H₂O temperatures. During January each of 13 study alligators exceeded $E_{\text{max}}$ substantially (by more than 6.3°C) at least once. The exploitation of solar-radiant energy is suggested by Fig. 2, which plots black-body temperature and temperature of a representative alligator against date-time. To facilitate visual interpretation, we graphed only 10-20 January. As expected, each spike in alligator $T_b$ inevitably co-occurred with a black-body high.

![Figure 2](image_url)

**Figure 2.** Line with more extreme values shows black-body temperatures; line with less extreme values shows $T_b$’s of a representative alligator.

Finding # 4: Although black-body highs may be a necessary condition for winter alligators’ thermal “spikes,” they are not sufficient. Indeed, the high alligator temperatures in January were somewhat eccentric to individual alligators.

Figure 2 (above) shows that not every black-body extreme was accompanied by a proportionally extreme $T_b$ for our example alligator. Nor was such correlation the case for any other study animal. Furthermore, different alligators, even in similar, proximate habitats did not always warm up at the same time. We illustrate this in Figure 3, which overlays January thermal plots for two female animals from ENP.

![Figure 3](image_url)

**Figure 3.** Overlay of January thermal plots for 2 females from ENP.
Similarly, among 9 CA alligators, T<sub>b</sub>'s of 7 animals (labeled A-G in Table 4) exceeded 30°C at least once during January. One animal warmed 13 times, but for the other 6, there was only one day on which more than one animal achieved ≥ 30°C. In other words, most alligators broke 30°C occasionally during January, but they tended to warm up on different days (Table 4).

**Table 4.** January dates on which T<sub>b</sub>'s of 7 CA alligators (labeled A-G) exceeded 30°C.

<table>
<thead>
<tr>
<th>Date</th>
<th>Animals warming to &gt; 30°C</th>
<th>Date</th>
<th>Animals warming to &gt; 30°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 Jan.</td>
<td>A</td>
<td>17 Jan.</td>
<td>F</td>
</tr>
<tr>
<td>7 Jan.</td>
<td>A</td>
<td>22 Jan.</td>
<td>A</td>
</tr>
<tr>
<td>10 Jan.</td>
<td>A</td>
<td>28 Jan.</td>
<td>F</td>
</tr>
<tr>
<td>11 Jan.</td>
<td>A</td>
<td>29 Jan.</td>
<td>A</td>
</tr>
</tbody>
</table>

**Finding #5: When clustered by thermal variables, alligators group by size.**

Cluster patterns and memberships varied in minor detail throughout the year, but typical 2-cluster solutions divided alligators by size. An example is Fig. 4. Only the 2-cluster solution is appropriate (according to the pseudo-F analysis as defined in the Appendix; Φ<sub>1,1</sub> = 61.4).

![Cluster Tree](image)

**Figure 4.** Cluster members are labeled by mass in kg and gender (F or M).

**Finding #6: Alligator size appears to affect T<sub>min</sub> (not T<sub>max</sub>) and perhaps INTENSE.**

Table 5 shows results of monthly regressions modeling T<sub>min</sub>, T<sub>max</sub>, and INTENSE, separately, as functions of alligator size. Models involving T<sub>max</sub> were never significant. T<sub>min</sub> was a positive, significant, function of size from November through June. This suggests that during much of the year, large alligators did not get as cold as small ones. During warm months larger alligators had less intense circadian thermal cycles than smaller ones. (That is, INTENSE was a negative, significant function of size in May, June, August, and September.)

**DISCUSSION**

South-Florida alligators are approximate thermal conformers throughout much of the year (Table 2 and Fig. 1). In spring, however, our animals warmed, relative to their surroundings. This thermoregulation may be associated with breeding and/or increased feeding (Mcllhenny, 1935; Neill, 1971). With large samples of known reproductive and non-reproductive females, researchers might sort out the relative importance of those 2 factors. During springtime, alligator daily thermal cycles also increased in intensity, relative to environmental
temperature cycles (Table 3). This phenomenon was probably driven by radiant energy—since correlations between black-body and alligator temperatures were highest in spring. In other words our data suggest, as most authorities have believed for years (McIlhenny, 1935; Neill, 1971; Brandt, 1989), that in springtime alligators increase body temperatures by basking. Furthermore, this activity seems less important during other seasons.

### Table 5. Linear regressions of thermal variables on alligator size. Mass is in kg; “mean low” is mean, for month indicated, of daily minimum $T_b$; “mean high” is mean, for month indicated, of daily maximum $T_b$; “day-cycle intensity” is magnitude of largest (daily) Fourier component; “N/S” indicates $P > 0.05$; N is all 13 alligators.

<table>
<thead>
<tr>
<th>Month</th>
<th>Slope / P-value</th>
<th>Slope / P-value</th>
<th>Slope / P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean low = f(mass)</td>
<td>mean high = f(mass)</td>
<td>day-cycle intensity=f(mass)</td>
</tr>
<tr>
<td>Nov.</td>
<td>0.07 / P = 0.011</td>
<td>N/S</td>
<td>N/S</td>
</tr>
<tr>
<td>Dec.</td>
<td>0.08 / P = 0.001</td>
<td>N/S</td>
<td>N/S</td>
</tr>
<tr>
<td>Jan.</td>
<td>0.07 / P = 0.005</td>
<td>N/S</td>
<td>N/S</td>
</tr>
<tr>
<td>Feb.</td>
<td>0.06 / P = 0.014</td>
<td>N/S</td>
<td>N/S</td>
</tr>
<tr>
<td>Mar.</td>
<td>0.06 / P = 0.024</td>
<td>N/S</td>
<td>N/S</td>
</tr>
<tr>
<td>Apr.</td>
<td>0.05 / P = 0.050</td>
<td>N/S</td>
<td>N/S</td>
</tr>
<tr>
<td>May</td>
<td>0.08 / P = 0.001</td>
<td>N/S</td>
<td>-0.06 / P = 0.026</td>
</tr>
<tr>
<td>Jun.</td>
<td>0.07 / P = 0.003</td>
<td>N/S</td>
<td>-0.08 / P &lt; 0.001</td>
</tr>
<tr>
<td>Aug.</td>
<td>N/S</td>
<td>N/S</td>
<td>-0.07 / P = 0.004</td>
</tr>
<tr>
<td>Sep.</td>
<td>N/S</td>
<td>N/S</td>
<td>-0.07 / P = 0.007</td>
</tr>
<tr>
<td>Oct.</td>
<td>N/S</td>
<td>N/S</td>
<td>N/S</td>
</tr>
</tbody>
</table>

In winter, alligator temperatures were usually at or below water temperatures, but $T_b$’s occasionally spiked to higher levels. These spikes were all associated with black-body highs (Fig. 2), but black-body highs did not inevitably bring $T_b$ spikes with them. Furthermore, different alligators spiked on different days (Fig. 3 and Table 4). These observations suggest that $T_b$ spikes result from alligator thermal “choices.” However, if alligators do not eat during winter (McIlhenny, 1935), then the temperature-spiking behavior would be energetically inefficient because raising $T_b$ would increase metabolic costs without apparent benefit (Colson and Hernandez, 1983; Lang, 1987; Lewis and Gatten, 1985; Peterson et al., 1993). Detailed observations of alligator food intake and metabolic activities might have helped explain winter $T_b$ spikes. Coulson and Hernandez (1983) state that alligators stop eating when body temperatures drop below 22°C. The spikes that we observed raised $T_b$’s far above this level, but only for a few hours. This brevity suggests that if food were acquired, it was digested very quickly—or that alligators were warming up for other reasons. The processing of metabolic wastes is one alternative explanation. Because our alligators could not lower winter $T_b$’s to the temperatures of more northern alligators, Everglades metabolic slowdowns may have been less profound. Perhaps, as a result, Everglades alligators must dump metabolic wastes more frequently. Raising $T_b$ to facilitate kidney function may be the most efficient way to deal with ionic and osmotic regulation (Minnich, 1982).

In cluster analyses based on thermal variables, alligators of similar size were grouped together (Figure 4). Also, in most months larger alligators had relatively high daily minimum temperatures and/or less intense circadian thermal cycles (Table 5). Surface/volume considerations suggest such phenomena, and many authors discuss the relationship between crocodilian size and thermoregulation (Spotila et al., 1973; Smith, 1975, 1976; Grigg, 1977; Johnson et al., 1978; Smith and Adams, 1978; Bartholomew, 1982; Grigg et al., 1998; Grigg et al., 1999). However, we were unable to investigate the social dimensions of thermoregulation, and if larger alligators have more choice of thermal microhabitats, then the effect of size on $T_b$’s may be socially mediated (Seebacher and Grigg, 1997). Since our 3 ENP alligators were larger than average, the apparent size effect might be confounded by area. Gender is another potentially confounding variable since our 3 males were also moderately large. (Despite reduced sample size, a significant size effect did persist in some months when we controlled for locality and gender. Gender and location were not in themselves significant.)

The development of implantable temperature recorders has not provided a panacea for research in crocodilian thermoregulation. An alligator’s environment presents a mosaic of thermal challenges and opportunities, and within that environment the animal must satisfy its non-thermal needs as well (Lang, 1987). To measure the thermal dimensions of an ENP alligator’s habitat would require data loggers (preferably in duplicate, at several depths) in every proximate hole, slough, and sawgrass flat—not to mention air-temperature
loggers, in sun and shade (preferably in physical models, with varying orientations to probable winds). The temperatures within an alligator may be almost equally complex (Pough and Gans, 1982), with variations between head, legs, trunk, and tail, perhaps mediated by complex blood shunts or other anatomic and physiological mechanisms (Turner et al., 1979; Bartholomew, 1982; Turner and Tracy, 1985; Lang, 1987). Thus the researcher should implant several loggers in each alligator. And the alligator-sample should be cross-classified by habitat, size, and gender, with sufficient replicates. Obviously the correlation of alligator and environmental temperatures would be more meaningful if the researcher recorded locations and behaviors of each animal (Seebacher and Grigg, 1997), preferably across several years since inter-annual variations in alligator habitat are substantial (Howarter, unpubl. data).

Perhaps such a research project could be funded for less than the cost of a major war, but we would not choose to be involved in it. Indeed, the present study suggests that mountains of data loggers and fleets of airboats are not our most critical research need. Instead, we must define thermoregulation questions more precisely and focus our study design more accurately upon such questions (Peterson et al., 1993). Toward these ends we solicit, and indeed covet, comments and suggestions from the broader crocodilian-research community.

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LITERATURE CITED


APPENDIX

A. Logger evaluation

At the time of our study, Onset’s Tidbit data loggers were available in two models, “narrow range” [-5°C to +37°C] and “wide range” [-20°C to +70°C]. We recovered and tested twenty loggers (Table A1). One had ceased functioning within < 1 day of implantation. All functioning loggers’ clocks were within 5 min of actual time at the study’s conclusion. Two wide-range loggers differed as much as 5°C from temperatures measured on a mercury thermometer. All data from unsatisfactory loggers were excluded from reported analyses. (Note: Based in part on information obtained during this study, Onset Computer Corporation has addressed problems in “wide-range” data loggers.)

<table>
<thead>
<tr>
<th>Logger Type</th>
<th># of Instruments</th>
<th>Deployment</th>
<th>Post-Study Evaluation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Narrow range</td>
<td>13</td>
<td>in alligators</td>
<td>satisfactory</td>
</tr>
<tr>
<td>Narrow range</td>
<td>1</td>
<td>in alligator</td>
<td>unsatisfactory (quit)</td>
</tr>
<tr>
<td>Narrow range</td>
<td>1</td>
<td>in environmental station</td>
<td>Satisfactory</td>
</tr>
<tr>
<td>wide range</td>
<td>3</td>
<td>in environmental stations</td>
<td>Satisfactory</td>
</tr>
<tr>
<td>wide range</td>
<td>2</td>
<td>in environmental stations</td>
<td>unsatisfactory (inaccurate)</td>
</tr>
</tbody>
</table>

Appendix table 1: Logger evaluation.

B. Defining variables

$G_{ave}$ is based on loggers from only 12 alligators. The thirteenth animal was consistently warmer than all others and, as an outlier, was excluded from the calculation of $G_{ave}$. We found no problems with her data logger. However, she had only three legs, and we feared that this might have affected her thermoregulation in some way. Duplicate analyses with other measures of “average” alligator temperature and other subsets of alligators did not produce qualitatively different results. (Note that we can also talk about the temperature of a given individual, $i^{th}$ alligator as $G_i$. In the text we usually refer to this variable as the $i^{th}$ alligator’s $T_b$.)

In defining E, we double-weighted deep H$_2$O because (1) shallow H$_2$O and shade temperatures were more ephemeral and were highly correlated (in a sense, they measure the same thing) and (2) we wished to give equal weight to environment in both study areas. Because of their extreme daily cycles we excluded black-body temperatures from this environmental measure and analyzed them separately. We duplicated all analyses using additional fragments of environmental data and other indices of environmental temperature; no results were qualitatively different.

$D_{ave}$ is merely the difference between average alligator temperature, $G_{ave}$, and environmental temperature index, E. Positive values of $D_{ave}$ indicate that, on average, alligators are warmer than their environment. (Note that we can also talk about the temperature of some individual, $i^{th}$ alligator relative to its environment: $D_i = G_i - E$, or $D_i = T_{b,i} - E$.)

INTENSE is the largest component in a Fourier decomposition of alligator temperatures (Wilkinson, 1996). Within an alligator’s year, the most intense thermal cycle is daily (this is hardly newsworthy; animals warm by day and cool by night). Therefore the magnitude of INTENSE reflects the intensity of alligators’ circadian thermal cycle. (Note that although INTENSE could be calculated on the time series of $G_{ave}$, we discuss INTENSE only as a variable associated with individual alligators.)

RATIO shows INTENSE divided by the largest Fourier component for environmental temperatures. This is done both for our environmental index, E, and for black body. The textual context makes the current usage clear. (Of course the largest Fourier component for E and for black body is daily; environmental temperatures warm by day and cool by night.)

We calculated the above variables across our entire study period. We also calculated monthly averages for E, $G_{ave}$, and $D_{ave}$. And we determined values for INTENSE by months.

$D_{smooth}$ is a running weekly median of D (either $D_{ave}$ or $D_i$; textual context makes the application clear). Recall that D would be measured 20 times per day, or 140 times per week. Thus, $D_{smooth, 1} = \text{Median} (D_1, D_2, \ldots, D_{140})$, and $D_{smooth, 2} = \text{Median} (D_2, D_3, \ldots, D_{141})$, etc.
\[ T_{\text{max}}, T_{\text{min}}, E_{\text{max}} \text{ and } E_{\text{min}} \text{ require no further definition.} \]

C. Cluster-analysis details

Our distance metric was Euclidean. We considered as interesting only clusters that replicated under both Ward’s and median-linkage methods (Milligan, 1980; Milligan and Cooper, 1985; Wilkinson, 1996; Wilkinson et al., 1996). On a cluster diagram of interest we determined the appropriate number of clusters to analyze by the following procedure.

1. Comparing cluster solutions. Begin with 1 cluster (all alligators in one group) and ask whether 2 clusters will explain appreciably more of the variance in clustering variables. (This is done by an analysis of pseudo-F statistics; see 2. and 3. below.) If the answer is “No,” then accept the 1-cluster solution. If the answer is “Yes,” then ask whether 3 clusters will explain appreciably more of the variance than 2 clusters. If the answer is “No,” then accept the 2-cluster solution. If the answer is “Yes,” then ask whether 4 clusters will explain more of the variance than 3 clusters….

2. Calculating an appropriate test statistic for comparisons. We call the relevant test statistic a pseudo-F, or \( \Phi \), because although the calculations resemble a conventional F-statistic, the data do not fit the underlying probability model of F. The pseudo-F statistic, \( \Phi \), is calculated as follows:

\[
\Phi = \frac{(\text{mean-square-model})}{(\text{mean-square-error})}, \text{ or } \\
\Phi = \frac{[(\text{SSED}_{c-1} - \text{SSED}_c)/(c-1)]} {[(\text{SSED}_c)/(n-(c-1)-1)]},
\]

where \( n \) is number of observations; \( c \) represents the number of clusters under consideration, and \( \text{SSED}_c \) and \( \text{SSED}_{c-1} \) represent sums of squared Euclidean distances around cluster centroids.

3. Choosing a cut-off value for \( \Phi \). Because \( \Phi \) is not an actual F-statistic, and because the underlying probability model is in any case unclear, P-values from conventional F-tables are not directly meaningful. Monte Carlo simulations (Beale, 1969) suggest that table “probabilities” \( \leq 0.005 \) προσδεόμενος χώρος ιπτερον τριαντάδας Χλωστικήσ. Της ταβλή προσβάσιμα τιπς φωνέτα Φ are read from standard F-tables; “degrees of freedom” are taken as \( c – 1 \) and \( n – c \).
Is Bone Surface Texture an Indicator of Skeletal Maturity in
*Alligator mississippiensis?*

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ABSTRACT: Recent studies of fossil archosaurs have noted changes in bone surface textures throughout ontogeny. Although the specific textures vary among different taxonomic groups, the general reported pattern is an overall reduction in surface porosity with increasing maturity. The use of predictable texture changes as ontogenetic indicators would provide a valuable tool for determining relative ages of fossil animals. At this time, however, the consistency of reported texture changes in both modern and extinct taxa is largely untested. The current study is part of a broader project evaluating utility of textural aging in the horned dinosaur *Centrosaurus* through analysis of the closest extant relatives of Dinosauria (Crocodilia and Aves). Results obtained to date suggest that although the method may be successfully applied to modern birds, it fails to distinguish relative age classes in *Alligator mississippiensis*. Controlling for additional factors suspected to affect textural variation—sexual dimorphism, seasonally interrupted growth, and wild versus captive lifestyle—provides little resolution. Indeterminate growth is certainly a factor; however, this alone cannot explain all observed variability. Until the factors affecting bone texture changes in modern crocodilians are better understood, it is recommended that this method be applied only with caution to studies of fossil taxa.

INTRODUCTION

A potentially promising method for assessing relative ontogenetic age of vertebrate fossils may be “periosteal aging” (*sensu* Sampson et al., 1997), which relies on the recognition of a fundamental distinction between immature and mature textures on bone surfaces. Such textural variations are considered macroscopic reflections of differences in the degree of ossification of immature versus mature skeletal material. It should be noted that the terms “immature” and “mature”, as used here, designate stages in the development and growth of the skeleton, and do not imply any assumptions regarding reproductive status.

Johnson (1977) reported textural differences in the humerus of immature and mature ichthyosaurs, noting a porous texture on immature bones in contrast to a smooth surface on mature elements. Degree of ossification has also been employed in distinguishing juveniles and subadults from adults among small theropod dinosaurs (Callison and Quimby, 1984) and pelycosaur (Brinkman, 1988). Bennett (1993) examined ontogeny in the long bones of pterosaurs, and described subadult bone as having a porous texture that was absent in adult specimens. Sampson et al. (1997) and Ryan et al. (2001) noted and defined three textural age classes in ceratopsian dinosaurs: a juvenile texture characterized by fine parallel striations generally oriented in the direction of growth, an adult texture characterized by the absence of the juvenile type, and an intermediate subadult texture comprising a mosaic of striated and non-striated regions. Carr (1999) applied the textural classes of Bennett (1993) and Sampson et al. (1997) to tyrannosaurid theropods.

Rapid bone growth has been hypothesized as the cause of the juvenile textures; adult bone texture is thus attributed to a cessation or at least dramatic slowing of growth (Bennett 1993; Sampson et al., 1997; Ryan et al., 2001). The presence of fine porosity and striations on actively growing immature bone may relate to ossification patterns and incorporation of vasculature into the matrix of growing bone (Enlow and Brown, 1958; Cormack, 1987). A reduction in these textures may therefore be presumed to occur during the aging process as growth rates decrease.

Generalized textural differences similar to those described in fossil vertebrates have been noted occasionally for modern species. Callison and Quimby (1984) examined long bones of immature and mature individuals from six extant bird genera. They noted lineations and surface exposure of spongy bone in immature elements; these became progressively fainter and disappeared as the birds matured. Sanz et al. (1997) noted the presence
of clusters of tiny foramina on the bones of a Cretaceous bird nestling, and compared these to similar patterns of grooves and pores caused by incomplete ossification of periosteal bone in modern birds. Johnson (1977) postulated that removal of the periosteum from the actively growing bone of young crocodilians would reveal a pitted surface texture, whereas a smooth surface would be revealed in older animals in which appositional growth had slowed.

The potential for using periosteal aging to provide reliable relative age estimates in fossil taxa seems theoretically reasonable, provided there is sufficient preservation of original bone surface (Tumarkin and Dodson, 1999). A detailed examination of the relationship between texture and skeletal maturity in modern taxa is necessary, however, before the periosteal aging method can be comfortably applied to fossils. This study aims to investigate the relationship between surface texture and bone growth in the American alligator Alligator mississippiensis. It forms part of a larger project considering the validity of the periosteal aging method for dinosaurs through examination of modern crocodilians and birds, the nearest living relatives of Dinosauria.

MATERIALS AND METHODS

Osteological collections were surveyed at the Royal Ontario Museum (ROM), Museum of the Rockies (MOR) and Florida Museum of Natural History (UF). The UF collection was further supplemented with a sample of postcranial bones obtained in cooperation with the Florida Game and Freshwater Fish Commission (GFC) during salvage of carcasses on Lake Griffin during spring and summer 2000. The total sample is a diverse collection of individuals of both sexes from multiple populations in Florida, Louisiana, and South Carolina. Effort was made to include only those animals for which sex, lifestyle, and season of death were known. Lifestyle is here classified as wild, captive, or farm. Animals coded as captive were raised under ambient light and temperature conditions in large enclosures allowing for normal mobility. Farm-raised animals were those confined in tanks under controlled temperature and light conditions. Wild crocodilians living in environments with seasonal temperature fluctuations undergo periods of slowed or arrested growth during the winter season of lower temperatures and lower food availability (Peabody, 1961; Enlow, 1969; Neill, 1971; Chabreck and Joanen, 1979; Andrews, 1982; Castanet al., 1993). For American Alligator, this period may vary somewhat throughout the species’ range but generally lasts from October or November through March (Neill, 1971; Chabreck and Joanen, 1979; Wilkinson and Rhodes, 1997; J.P. Ross; Pers. Comm. 2000). For purposes of this study, animals were classified as having died during one of three seasons: an inactive season of November through March, an active season of May through September, and a transitional season of April and October. The transitional class was created as an attempt to account for geographical and possible yearly variation in duration of the inactive season.

All captive and farm-raised animals died within the active season. Accordingly, no adjustment was needed to reflect the fact that these individuals may have experienced more constant growing conditions than their wild counterparts.

Bone surface textures on femora, tibiae and humeri were documented through a combination of detailed description, sketches and photography. Preference was given to right side elements; left elements were used in cases where the right was missing, damaged post mortem, or pathologic. A texture scale, ordered based on decreasing surface porosity and independent of specimen age and size, was developed for each limb element. Within this spectrum, a texture code was then assigned to each individual bone.

Two independent methods were used to estimate relative age and skeletal maturity of individuals. The first used femur length (measured from the most proximal point on the femoral head to the distalmost point on the lateral condyle) as a proxy for overall size of the individual, following studies by Dodson (1975) and Farlow (unpublished data, Pers. Comm., 2002). Relative body size was then employed as an estimate of relative age and skeletal maturity. Estimates of relative ages based on total body length may be unreliable for Alligator, however, due to potential variation in size and/or growth rates between sexes and among habitats and geographical regions (McIlheny, 1935; Peabody, 1961; Bellairs, 1970; Neill, 1971; Andrews, 1982; Jacobsen and Kushlan, 1989;Magnussen et al., 1989; Castanet al., 1993; Woodward et al., 1995; Dalrymple, 1996; Wilkinson and Rhodes, 1997). Sex and geographical region were known for the majority of the study sample; variation due to other factors could not be controlled for in the collections examined. A second, size-independent, method for relative age estimation was therefore attempted.
The method used here is a modified version of that designed by Brochu (1996) to determine ontogenetic transformation series for *Alligator* appendicular bones. Character matrices were constructed based on presence/absence data for muscle scars and other bony landmarks present in the largest and presumably oldest animals. The characters employed here are identical to those outlined by Brochu (1996). These ontogenetic matrices were treated in an analogous fashion to phylogenetic matrices and were subjected to a parsimony analysis using the branch and bound algorithm of PAUP, version 4.0b10 (Swofford, 1999). The outgroup was a hypothetical embryonic stage coded as a form lacking all bony landmarks considered. In cases where more than one most parsimonious tree was obtained, a strict consensus tree was generated to identify those nodes present in all trees. Only the character changes associated with the consistent nodes were treated as representing discrete ontogenetic stages. Characters undergoing reversals and homoplastic characters with variable occurrences were discarded as unreliable indicators. The remaining characters are those that consistently appeared in a predictable order during ontogeny. Based on this transformation series, the ontogenetic status of any given element from a particular skeleton could be expressed as a percentage of the total number of stages through which that element must pass before attaining full maturity. This value, here termed “percent maturity”, corresponds to the “transformed stage” of Brochu (1996).

Bone texture codes were then correlated with both femur lengths and percent maturity values to assess whether a recognizable pattern of textural changes occurs during *Alligator* ontogeny.

**RESULTS AND DISCUSSION**

Although identical analyses were performed for the femur, tibia, and humerus, only results for the femur are reported here. Preliminary examination of data for the tibia and humerus suggests similar results.

**Texture Codes**

Twelve distinct combinations of surface textures were recorded from the femora examined. These may be grouped into seven major types. It should be noted that in all individuals, certain regions consistently retained a coarser texture than surrounding surfaces. The fourth trochanter and surrounding attachments of *m. coccygeofemoralis longus* and *brevis* are rugose (Romer, 1923; Dodson, 1975; Brochu, 1996), marked by large open pits and pores. The proximal dorsal surface bears an area of strong fibrous texture and parallel ridges and furrows (proximal dorsal tuberosity of Brochu, 1996). Similar rugose ridges are found on the medial and lateral sides of the distal condyle. The proximal ventral surface also tends to have a radiating fibrous and porous texture. These sites are hereafter collectively referred to as regions of persistent coarse texture. Additionally, the longitudinal ridges for attachment of the adductor musculature and *m. iliofemoralis* (Romer, 1923; Brochu, 1996) often preserve distinct porosity when surrounding regions are smoother.

Textural patterns for Alligator femora are described below. Roman numerals denote the seven major texture types. Numbers in parentheses indicate numerical values assigned to each major type and its subtypes for purposes of graphing the textural spectrum.

Type I. This type is characterized by the presence of a “fuzzy fibrous” texture covering nearly the entire bone. The surface lacks distinct pores, but is markedly grainy and generally rough to the touch. (1)

Type II. This type is characterized by the presence of “etched porosity”, a condition in which visible pores penetrate the bone surface at variable angles and are often connected via shallow surface grooves. This results in a disorganized, etched appearance midshaft. As the proximal and distal ends are approached, porosity may become more organized, with pores piercing the surface on an angle to form fibrous or striated regions radiating toward the bone ends. Type II bones are divided into two subtypes: one in which the porous texture extends over the entire shaft (2), and one in which porosity fades out to smooth areas proximally and distally (2.5).

Type III. This type is characterized by the co-occurrence of etched porosity and “dotted porosity”, a more organized porous condition in which pores penetrate the bone surface at roughly right angles to the shaft. With no discernable pattern, the two types of porosity either occur independently on distinct areas of the bone, or overlap each other in the same region. As with Type II bones, the angle of the pores may change along the shaft to create radiating fibrous or striated regions proximally and distally. Type III bones are divided into three subtypes: one in which porosity covered the entire shaft (3), one in which
porosity fades out into smooth areas proximally and distally (3.33), and one in which porous texture shares the midshaft region with seemingly randomly placed large smooth areas (3.67).

Type IV. This type is characterized by the presence of dotted porosity in the absence of etched porosity. As with Types II and III, radiating fibrous and/or striated areas may occur proximally and distally. Three subtypes occur (4, 4.33, 4.67); these are defined by the same relative distributions of porous and smooth areas as the subtypes for Type III.

Type V. This type is characterized by a grossly smooth surface texture, except in the regions of persistent coarse texture described above. Faint shallow dimples may be visible in some areas, but these are not associated with pores that penetrate the bone surface (5).

Type VI. This type is shows a “muting” of coarse textures in the persistently coarse areas. Ridges and furrows are still present in these areas, but are not as well defined as in previous textural types, and are generally not associated with penetrating pores. The rest of the shaft shows a dotted porous texture, but with the pores more widely scattered than in the dotted textures of types III and IV (6).

Type VII. This type occupies the least porous point on the texture spectrum, combining the smoothest features of types V and VI. This type is characterized by co-occurrence of a grossly smooth or faintly dimpled shaft with muting of textures and loss of porosity in the persistently coarse regions.

Estimates of Skeletal Maturity

Use of Brochu’s (1996) method and characters to determine percent skeletal maturity yields a transformation series of five stages (Table 1). Stage 1 is equivalent to a hypothetical embryonic or moment-of-hatching stage lacking all scored characters and is therefore assigned a percent maturity value of zero. Thus stages two through five equate to percentages 25, 50, 75, and 100, respectively.

Table 1. Transformation series of ontogenetic stages resulting from parsimony-based character analysis after Brochu (1996).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Defining Characteristics</th>
<th>Percent Maturity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Absence of defining characteristics of Stages 2-5</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>Appearance of medial scar for <em>m. puboischiofemoralis internus</em>, <em>pars dorsalis</em></td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Absence of defining characteristics of Stages 3-5</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Appearance of lateral scar for <em>m. puboischiofemoralis internus</em>, <em>pars dorsalis</em></td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>Absence of defining characteristics of Stages 4-5</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Appearance of proximal condylar fold</td>
<td>75</td>
</tr>
<tr>
<td></td>
<td>Appearance of rugosity on medial and lateral sides of distal condyle</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Appearance of longitudinal scars for <em>m. iliofemoralis</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Absence of defining characteristics of Stage 5</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Appearance of lipping of finished condylar bone over shaft</td>
<td>100</td>
</tr>
</tbody>
</table>

Unfortunately, the method shows itself to be not particularly useful for analysis of this sample, as only six of thirteen scored characters are informative, and these are all acquired very early in ontogeny. With two exceptions, all femora with a length greater than 33 mm are scored at stage five, or 100 percent mature (Fig. 1). The presence in Fig. 1 of two larger femora scored at stage 4 is misleading. The ends of these bones were eroded post mortem such that the presence or absence of the character diagnostic of stage five (lipping of finished condylar bone over shaft) could not be evaluated. They were therefore scored at stage 4 as the last stage to which they could be definitively assigned. Distribution of the rest of the sample, however, suggests that these individuals should more rightly be scored as Stage 5. Although it is of some interest that a repeatable sequence of character acquisition is confined to early ontogeny, it is not helpful for ontogenetic interpretation of
surface textures, since 94.5 percent of the sample, comprising animals of a large range of body size and textural variation, falls within the “100 percent maturity” range.

Correlation of Texture and Size / Skeletal Maturity

The size-based analysis of the total sample (Fig. 2a) reveals several notable points. Texture types I and II appear restricted to small animals of femur length less than 70 mm. Animals of the largest size classes (femur length greater than 240 mm) appear restricted to texture types IV through VII; this corresponds to a complete absence of the fuzzy fibrous and etched porous textures. Types III and IV may represent successive stages, with the co-occurrence of etched and dotted porosity (Type III) eventually giving way to dotted porosity alone (Type IV), but the amount of overlap between the two fields is considerable. The wide range of sizes over which Types III through VII occur makes them of extremely limited utility for estimating ages of isolated bones. This assumes, of course, a good correlation between size and chronological age, which may not be the case (see below). Unfortunately, the size-independent analysis (Fig. 2b) does little to clarify this picture. As stated above, 94.5 percent of the entire sample falls into maturity code five, masking most of the variations visible in the size-based analysis.

![Figure 1](image.png)

**Figure 1.** Relationship between femur length and percent skeletal maturity of femur as determined by parsimony-based methods.

As stated above, a number of factors may contribute to growth variation in *Alligator*, and thus the decoupling of size and chronological age. These may include sexual dimorphism; seasonally interrupted growth; environmental conditions of habitat, diet, and temperature; and indeterminate growth (McIlhenny, 1935; Peabody, 1961; Bellairs, 1970; Neill, 1971; Andrews, 1982; Jacobsen and Kushlan, 1989; Magnussen et al., 1989; Castanet et al., 1993; Woodward et al., 1995; Dalrymple, 1996; Wilkinson and Rhodes, 1997; Elsey et al., 2000; Lance et al., 2000). To the extent possible, effort was made to control for these variables within size-based analyses of the study sample.

Sexual Dimorphism

Previous studies of American Alligator have reported larger adult sizes for males relative to females, as well as sexual dimorphism in growth rates (e.g. McIlhenny, 1935; Bellairs, 1970; Neill, 1971; Chabreck and Joanen, 1979; Magnussen et al., 1989; Woodward et al., 1995; Wilkinson and Rhodes, 1997), such that average growth rate in females decreases relative to that of males after a certain point in ontogeny. Chabreck and Joanen (1979) report that in wild individuals from Louisiana, growth rates in both sexes are similar until roughly three years of age. Although growth in both sexes gradually begins to decrease after the first year post-hatching, after age
three this decline is more pronounced in females. Sexually dimorphic growth rates may confound a size-based analysis of textural trends, due to the potential for lumping younger faster growing males with older more slowly growing females in the same size range.

Figure 2. Relationship between textural types and femur length (A) and parsimony-based percent femoral maturity (B). Areas of circles in graph B represent the number of individuals plotting at each location.

Restricting the size-based analysis to individuals of known sex (Fig. 3), however, does little to reduce the high variability of texture type distributions. Examination of Figure 3 does little more than confirm that males of *Alligator* reach a larger adult size than females. Texture types III through VII still occupy wide overlapping size ranges in both sexes. The distinction between types III and IV may be more clearly defined when only males are considered; this however may also purely reflect sample composition.
**Figure 3.** Effect of sexual dimorphism on relationship between textural types and femur length.

### Interrupted Growth

In the bone of wild crocodilians, seasonal variations in growth rate are visible histologically as zones and annuli and/or lines of arrested growth (LAGs). Zones are vascularized regions deposited during seasons of active growth. Annuli comprise thinner sparsely vascularized or avascular lamellae deposited during periods when growth has slowed. LAGs, as their name implies, are rest lines formed during a hiatus in growth (Enlow and Brown, 1957; Peabody, 1961; Enlow, 1969; Ricqlès, 1974, 1976; Buffrenil, 1980; Castanet et al., 1993; Castanet, 1994). These histological features have also been documented in captive crocodilians living under more-or-less constant conditions, although they may not be as pronounced as in wild individuals (e.g. Buffrenil, 1980). Since the immature textural types described in previous studies are associated with active osteological growth processes, it might be surmised that an individual dying during a period of slowed or arrested growth would not exhibit these textural features, regardless of overall skeletal maturity (Tumarkin and Dodson, 2000, 2001).

Surprisingly, factoring season of death into the analysis (Fig. 4) lends no additional resolution to the data set. One might argue that this reflects the fact that individuals dying during the transitional and inactive seasons comprise a limited portion of the total sample (4.6 and 5.5 percent, respectively). It is notable, however, that the 89.9 percent of individuals dying during the active season occupy the full range of textural variation seen in the total sample.

### Lifestyle and Geographical Range

Individuals of *Alligator* raised in captivity under optimum conditions of temperature, nutrition, etc. have shown the potential for higher sustained growth rates than wild individuals (e.g. Buffrenil, 1980; Elsey et al., 2000). It is also possible for captive animals to experience retarded growth rates relative to their wild counterparts if nutritional and temperature requirements are not met, or as a result of other stresses such as crowding (e.g. Lance et al., 2000). It is therefore a reasonable hypothesis that captive or farm-raised animals may show a different distribution of texture types than wild individuals.
Figure 4. Effect of season of death on relationship between textural types and femur length. Active=May through September; Transitional=April and October; Inactive=March though November.

As with the considerations of sexual dimorphism and season of death, however, this hypothesis is not supported by the data (Fig. 5). Although captive individuals account for the largest individuals of both sexes in the study sample (compare Figs. 3 and 5), the distribution of texture types is similar to that in the smaller wild individuals. Thus, removal of the captive animals from the sample would do little to reduce variability of texture with respect to size. Farm-raised individuals all exhibit texture Types III and IV; however, this distribution is consistent with that of wild and captive individuals of similar size.

Figure 5. Effect of lifestyle on relationship between textural types and femur length. See text for distinction between captive and farm-raised individuals.

Previous studies of *Alligator* growth have concluded that growth rates vary throughout the species’ geographical range due to local environmental conditions and resource availability (Jacobsen and Kushlan, 1989; Dalrymple, 1996; Wilkenson and Rhodes, 1997). It may therefore be fruitless to employ size as an age
proxy for a sample drawn from diverse geographical areas. Geographical variation in growth rates, combined with sexual dimorphism, may account for some of the variability observed in the femur length versus texture plots. The study sample examined here included individuals from Florida, Louisiana, and South Carolina. The South Carolina sub-sample included only three individuals, all hatchlings, and was excluded from the geographical analysis. Separate analysis of wild Louisiana individuals (N=21) yields a distribution comparable to that obtained in the total sample analyses. The plot of wild individuals from Florida, however, yields a potentially interesting result (Fig. 6). Although distribution of textural types among males remains variable, there does appear to be a trend among females for a decrease in surface porosity with an increase in body size. It may be that an earlier and greater slowing of growth in female individuals is responsible for the presence of a pattern in this sex which is absent among the males, although with such a small female sample size (N=13) the pattern may also be sampling artifact.

**Indeterminate Growth**

Although growth in *Alligator* is often described as indeterminate, this does not mean that an individual alligator continues growing at a constant rate throughout life. As noted above, growth rates in females decrease relative to those in males. Growth rates also appear to eventually decrease further in both sexes, becoming nearly asymptotic after total lengths of 2.5 to 3.5 meters are attained in females and males, respectively (Woodward et al., 1995; Wilkinson and Rhodes, 1997). One might expect that a prolonged period of growth may cause so-called immature porous textures to be highly persistent throughout ontogeny (Tumarkin and Dodson, 2000). Although this may explain the occurrence of relatively porous texture types such as Type III in larger individuals, it does little to account for the reverse phenomenon, that is, the persistent occurrence of low porosity texture types such as Types V through VII in smaller individuals.

![Figure 6. Effect of sexual dimorphism on relationship between textural types and femur length for wild individuals from the Florida subset of the total sample.](image)

**SUMMARY AND CONCLUSIONS**

The data presented here suggest that the association between bone texture and skeletal maturity in *Alligator* is highly variable, even when sex, season of death, and habitat conditions are taken into account. It should here be noted that a companion study on the Canada goose *Branta canadensis* using identical methodology revealed an excellent correlation between textural types and age based on element size and date of death. In *Branta*, juveniles, subadults, and adults were clearly identifiable by distinct suites of textures with little to no overlap between groups. The growth regime of *Branta* individuals, which experience determinate growth and reach full adult size within one growing season, is, of course, in strong contrast to that of *Alligator*. The success of the
Branta analysis, the results of which will be reported elsewhere, strongly suggests that growth regime may be an important controlling factor in determining the reliability of the periosteal aging method.

Controlling for several sources of growth variation in Alligator (i.e. sexual dimorphism, season of death, lifestyle, and geographical range) does little to resolve the extreme variability in the Alligator sample. Indeterminate growth alone fails to account for all observed variation, particularly the repeated occurrence of low porosity textures in individuals of smaller size classes. It may be that a high sensitivity to local and regional environmental conditions, coupled with long periods of time to reach full adult size, renders growth in Alligator too variable to successfully apply the periosteal aging method at the species level.

Regardless of the specific controlling factors, the high degree of variation suggests that bone surface textures should not be relied upon as universal indicators of skeletal maturity, at least not in taxa with growth regimes resembling that of the American alligator. Until such time as the controlling factors are better understood, the application of the periosteal aging method for the aging of fossil specimens, especially those for which growth regime is unknown, is not recommended.

ACKNOWLEDGEMENTS

The following individuals and institutions generously granted access to study osteological material under their care: F. Wayne King, J. Perran Ross, and Kenneth Krysko (UF); Hans-Dieter Sues and Kevin Seymour (ROM); Cynthia Marshall (MOR). J. Perran Ross supervised salvage of Lake Griffin animals under the auspices of FWC and Special Use permit WX01261; Allan Woodward granted use of GFC facilities for initial processing of salvaged material. James Farlow initially invited access to the MOR sample and provided access to unpublished body-size data for those animals. Ruth Elsey, Grant Hurlburt, and Diane Borden-Billiot provided locality and habitat data for many individuals from the MOR and UF samples. Chris Brochu provided access to unpublished supplemental data for the parsimony analysis. Chris Brochu, Tom Carr, Peter Dodson, Barbara Grandstaff, and Matthew Lamanna provided much stimulating and informative discussion. Portions of this research were supported by The Jurassic Foundation, The Paleontological Society, Sigma Xi, University of Pennsylvania Paleobiology Stipends, a National Science Foundation Graduate Research Fellowship, and National Science Foundation Grant EAR 95-06694 to Peter Dodson.

LITERATURE CITED


Shunting in Alligators – Does it Make a Difference?
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ABSTRACT: Unlike other reptiles, crocodilians have a completely divided heart but have retained the ability to shunt right ventricular blood to the body via the left aorta (LAo). The LAo continues posteriorly and supplies the digestive system with right ventricular blood during shunting. This study focuses on the functional significance of shunting right ventricular blood to the digestive system in Alligator mississippiensis. Two groups of alligators were used in this study. One group had their left aorta surgically tied off and cut (LAo cut; unable to shunt) and the second group had sham surgeries performed on them (LAo intact). During fasting, serum glucose levels, blood pH and PCO₂ values and metabolic rates were similar in the two groups of alligators, as were the rates of mass loss. During feeding, growth rates were similar. Respiratory exchange ratios were significantly higher in alligators with their LAo cut. Differences were also seen in blood pH and blood PCO₂ measurements as well as in digestion rates. In conclusion, the ability to shunt right ventricular blood to the gut affects acid-base regulation as well as the digestive state in alligators.

Sexual Maturity in Male American Alligators:
What Can Plasma Testosterone Tell Us?
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ABSTRACT: Male American alligators are generally considered to reach sexual maturity at a total body length of about 180 cm. This estimate is based on examination of the reproductive tracts or by checking for the presence of sperm in the penile groove during the breeding season. We initiated this study to see if circulating testosterone levels correlated with presumed size of sexual maturity in male alligators. Blood samples were collected from wild caught alligators at Rockefeller Wildlife Refuge over a two-year period in every month of the year. Following sampling the alligators were marked and released. A total of over 1,300 blood samples was collected from male alligators as small as 60 cm and as large as 380 cm during the study period. The data were arranged, by month and by size classes. To our surprise, all samples had measurable testosterone and all showed a seasonal cycle similar to the cycle of large breeding males. However, there was an enormous difference in peak testosterone values in April and May. Peak values in the smallest size class reached only 0.7 ng/ml, whereas peak values in the largest size class were over 70ng/ml. There was a clear positive association between total length and plasma testosterone and no clear indication of when an animal was capable of breeding.
Reproductive Cycle of the American Crocodile and its Environmental Influences. Preliminary Results

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ABSTRACT: The main objective of this project is to understand how environmental factors affect breeding cycle, analyzing sexual hormones and plasma variables in adult American crocodiles to compare between the wild and captive for the management and conservations of the species. Here we present preliminary results of hormonal levels.

Captures and recaptures from 123 wild and captive American crocodiles of both sexes (1.8 – 4.44 m) were made since January to June of 2002 to bleed every month. Manzanilla” estuary in the coast of Jalisco, and in captivity at Crocodile Reproductive Center at San Blas (CRSB), Nayarit, Mexico. The project covers the reproductive cycle of the species.

Also environmental parameters were recorded. Sexual hormones of both sex were analyzed at the Center for Reproduction of Endangered Species (CRES) in San Diego, CA.

Key words: C. acutus, environment, hormones, reproductive cycle, México.

INTRODUCTION

Several attempts still development to understand more about the reproductions of the order crocodilia, in order to apply such information to management and conservation in several species. No studies of hormones exist in the American crocodiles to study breeding cycle, neither studies to understand the influences of the environmental factors in the reproduction of crocodilians concerning with hormones.

The American alligator have been study for many years to understand the breeding cycle analyzing hormones (Lance, 1987). Also some environmental factors of the environment have been correlated with the reproduction of some species but, at global level as C. intermedius (Thorbjarnarson and Hernández, 1993b) and one or few factors of the environment have been correlated with the breeding cycle of C. intermedius (Thorbjarnarson and Hernández, 1993a).

This time we present preliminary results of plasma steroids hormones in males (testosterone) and females (estradiol) in the American crocodiles during six months (January to June of 2002). More studies will be developed in the short future for stress hormone (testosterone) to correlate with sexual steroids and plasma chemistry will developed, as well, with the goal of understanding how and which of the environmental factors influences reproduction of the species by the hormone analysis and its implications for management and conservation of the species, in captive and in the wild to apply this information for the conservation and management of the species, supported by the information available for the species in our area (Ponce and Huerta, 1997; Huerta et al., in preparation).

MATERIALS AND METHODS

In order to study the relations of the breeding cycle of the American crocodile with the environmental factors during six months (January to June of 2002), covering the breeding cycle of the species, 123 individual were captured and recaptured in the wild and in captive. The sizes, total length (LT) ranges from 1.98 to 4.44 m in the wild and 2.20 to 3.40 m in captive. Also snout vent length (SVL) were recorded as follows: since the tip of
the snout to the rear of the tight, when the tight was at 90 degrees in angle from the body. Every measurement (TL, SVL) was taken always on the dorsal side of each animal, for this reason the measurements would be lightly skewed. This (SVL) measurement coincides with anterior vent measurement, standard in cocodrilians. The sampling site in the wild was La Manzanilla estuary in the municipality of La Huerta, south western in the coast of Jalisco. This crocodile population is considered the second best population of the species in the state (Ponce and Huerta unpublished data). Captive sampling site was at Crocodile Reproductive Center at San Blas (CRSB), in San Blas, municipality of Nayarit.

During every capture stress time was recorded - since acute stress begun to the end of blood extraction - this data were tanked into account since the reports that concentrations of stress hormone (corticosterone) increase during acute stress and also is known that an increase of corticosterone produces a decrease in the secretion of gonadal steroids in reptiles (Elsey et. al., 1991; Lance and Elsey, 1986).

The analysis of the testosterone in males and estradiol in females were made at the endocrinology division laboratory of Center for Reproduction o Endangered Species in San Diego, CA. Using radioimmuno assay technique. 50 microliters of testosterone and 100 microliters of plasma for estradiol were utilized during every assay following the technique of Schramm et al. (1999).

Environmental factors and vent temperature were taken as well, in order to correlate this factors with concentrations of steroids during every month. Using data loggers, light intensity, water and air temperature and humidity were recorded on every sampling locality. Water level and salinity were recorded in the wild every month.

Anova analysis were made to analyze hormonal concentration with computer software Stat Graphics in order to understand if there are some differences in the reproductive cycle between captive and in the wild American crocodiles.

n123 Captures and recaptures
n63 Wild 1.98-4.44m
nMean 3.07m
n61 Captive) Jan-Jun 2002 (1st two weeks)
Mean 2.63; Min 2.20, Max 3.40
nTime of stress
11:36 min W
7:42 min C

Results and discussion

Testosterone levels in wild crocodiles were significant different from those from captive (P< 0.05; F= 5.96) (Fig. 1), but not differences was recorded in estradiol concentrations (Fig. 2). Estradiol levels were quite low compared with American alligator. Highest testosterone mean value (January) for American crocodiles is 11.82 ng/ml (Fig. 3), lower than reported for American alligator, which mean highest testosterone value rise on April with almost 50 ng/ml. Highest mean value of Estradiol during in January (9.5 pg/ml) in American crocodile (Fig. 4) is quite lower than highest value reported for American alligator, near 600 pg/ml (Lance, 1989).

As unexpected higher testosterone level in American crocodiles was in January decreasing in February and falling since March to June with low hormonal levels. Females shows higher estradiol levels from January to March falling on April, showing the beginning of nesting season. Estradiol values begun to rise every month with levels similar to February. Testosterone concentrations suggest breeding at February but estradiol suggest in March. Last coincides with the observations of Lance (1989) who suggest that mating time is two or three weeks before nesting in American alligator. There is some differences observed in the nesting season. In captive, nesting season begun during early April and in the wild late April. Mating time in captive is observed, with monthly hormonal values in one male during six months (Fig.,5) but , monthly hormonal levels in captive females is not representative (data not shown). This information suggest that mating season in captive is during late February to March and nesting time since early/unti late April. With the observed nesting in the wild and captive and mating time in the wild, peak mating time in the wild is during March.
Testosterone differences between captive and wild crocodiles, could be due to stress, because dominant males push to the submitted animals out of the pen most of the time and during breeding season aggression are common from alpha males to submitted animals. Something similar was observed in nesting females.

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LITERATURE CITED


Stress Responses to Noosing and Restraint versus Capture by Electrical Stunning in Captive Crocodylus porosus
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ABSTRACT: The aim of this study was to compare and evaluate the stress responses and welfare of captive estuarine crocodiles, Crocodylus porosus to electrical stunning, as opposed to the traditional capture and restraint methods of noosing and roping animals. Electrical stunning equipment recently developed and built by the Department of Primary Industries in Australia was used to stun 2-2.4 m crocodiles. A 110 V charge was delivered for 4-6 seconds via a set of metal forks applied to the back of the animal's neck. Crocodiles were rapidly immobilized during stunning, which was followed by 5-10s of rigor and tail twitching after which the animals were completely relaxed with legs splayed backwards, parallel to the body. Crocodiles remained incapacitated for 5-10 minutes, allowing animals to be handled and measured. Blood samples were taken from stunned and noosed animals immediately upon immobilization or capture and after 30 min, 1, 4, 12, 24 and 48 hours of recovery. Blood was taken from the cervical sinus in heparinised syringes, and haemoglobin and haematocrit concentrations measured. Plasma samples were analysed for corticosterone, glucose and lactate levels. The stress response of stunned animals was significantly reduced compared to manually captured crocodiles. Time course of changes in the various blood parameters will be presented.

Ultrasonography of Reproductive Structures and Hormonal Correlates in the American Alligator, Alligator mississippiensis: Application to Population Studies
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ABSTRACT: Ultrasonography has been used effectively to study reproduction in a variety of reptile species however its application to crocodilians has been relatively limited. In this study we present results from a pilot study testing the efficacy of using ultrasonography to monitor reproduction in the American Alligator, Alligator mississippiensis. Ultrasound results were then compared with hormone results. A total of 65 females were examined by ultrasonography during April, May and June. Ultrasound results were validated on a series of reproductive females (n=14) necropsied for other studies. Vitellogenic follicles, recently ovulated eggs, fully developed well calcified eggs and atretic follicles were readily discernible with ultrasound in reproductively active females. Reproductive structures were observed in 27 females of which 20 were actively reproductive while 7 were non-reproductive containing large atretic follicles. Oviducts were discernible in females with eggs. Ovarian state was also correlated with hormone levels. Ultrasonography can be used to accurately assess reproduction in wild populations and provide data to estimate the number of reproducing females in a given year.

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**ABSTRACT:** Ecomorphology is an integrative discipline that focuses on understanding the relationships among the morphology, ecology, and behavior of organisms. Its primary precept is the incorporation of whole-animal performance measures (e.g., bite force, sprint speed) into studies that attempt to relate morphology to ecology and behavior (Arnold, 1983). All crocodilians undergo considerable growth coupled with complex ontogenetic morphological changes of the trophic apparatus. At the same time major dietary shifts occur. How morphological changes are related to dietary shifts requires an understanding of the biomechanics of the system (e.g., bite-force performance, mechanical relationships, dental material properties). We conducted a feasibility study to measure bite-force performance in a large crocodilian throughout ontogeny. Using a series of precision force transducers, we made measurements of bite force on 41 captive *Alligator mississippiensis* individuals ranging from hatchlings to large adults. This shows that quantification of bite-force performance in these large reptiles is feasible. How bite-force performance scales with respect to measurements of body size was determined for these individuals. Also, bite force throughout development was examined in light of ontogenetic changes in trophic ecology. The results show a 800-fold range (12–9452 N) in bite force. Bite force through ontogeny showed positive allometry with respect to body size. The overall pattern of allometric bite force increase throughout ontogeny did not correlate discreetly with major dietary shifts.

**INTRODUCTION**

Ecomorphology is an integrative discipline that has emerged from the desire to understand how morphological variation causes, shapes, influences, or affects variation in the ecology and behavior of organisms. Its principal tenet, delineated by Arnold (1983), is the incorporation of whole-animal performance measures (e.g., bite force, sprint speed) into studies that attempt to relate morphology to ecology and behavior. A measure of whole-animal performance should be chosen based on its promise to provide clues as to how morphological variation of the focal system may impose constraints onto an ecological or behavioral parameter. Alternatively, there should be an indication that the selected whole-animal performance measure provides a means to broaden the scope of opportunities in an ecological or behavioral sense. In addition, the performance measure should be tractable. It must be readily measurable, repeatable, and amenable to comparison among species.

Bite-force performance is a whole-animal performance measure that can potentially provide insight into the feeding biology of a variety of taxa. Bite force contributes to limiting or expanding the potential to include certain prey items in the diet. Among crocodilians, the American alligator, *Alligator mississippiensis*, provides an excellent system for an intraspecific ecomorphological investigation of the ontogeny of feeding biology for several reasons. First, *A. mississippiensis* spans a considerable size range from hatchlings to adults. At birth alligators weigh about 0.605 kg but can reach 275+ kg late in adulthood (Woodward *et al*., 1995). Second, during this remarkable 4000-fold increase in mass, the trophic apparatus exhibits notable changes in shape. For example, the short and broad snouts of hatchlings elongate and become relatively more slender (Dodson, 1975). Also, the caniniform teeth of hatchlings progress from a delicate and sharp morphology to a blunt and robust
form in adulthood. Similarly, the distal teeth (i.e., those toward the back of the jaws), which are initially sharp-edged and blade-like, become bulbous and molariform (Edmund, 1962). Third, the diet of the *A. mississippiensis* undergoes substantial change during ontogeny (Dodson, 1975). The dietary ontogeny of *A. mississippiensis* shows that, as alligators grow, they include prey in their diet with increasingly hard and rigid elements (e.g., integument, bones). Finally, as we demonstrate in the present study, measurement of bite-force performance in *A. mississippiensis* is feasible and can be used to make ties to the feeding biology of this species.

Although many studies have documented the diets and functional morphology of crocodilians, virtually no empirical data have been garnered on the actual biomechanical performance of the jaws and associated musculature (e.g., bite force) and teeth (e.g., sharpness, pressure generation). These measures provide the essential ties between these data sets and are critical to gaining a comprehensive understanding of how the phenotype of these animals relates to their realized ecological niche. Despite the inherent difficulties of working with large carnivorous reptiles, a few pioneering attempts to assess bite force in crocodilians have occurred. Sinclair and Alexander (1987) included a sub-adult (1 m TL) caiman (*Caiman crocodilus*) in their analysis of reptilian bite force. Following their lead, Vliet (cited as a personal communication in Erickson *et al.*, 1996) tested a prototype mechanical bite bar on a large adult *A. mississippiensis*. Although a potential design flaw precluded ultimate implementation of the device, the test showed that powerful snapping bites could be elicited from adults of the species.

Building upon the results of these efforts, we recorded bite-force performance throughout ontogeny in a complete growth series of *A. mississippiensis* using a series of precision electronic bite-force transducers. Post-testing measurements of snout-vent length and body mass then were made on each specimen to examine the relationship between bite-force performance and growth.

**MATERIALS AND METHODS**

**Specimens**

To quantify the ontogeny of bite-force performance in *A. mississippiensis* and explore its relationships to growth and dietary ontogeny, we procured 53 animals ranging from hatchlings (0.30 m TL) to large adults (3.7 m TL). Of these, 41 produced useable performance measures (see below). Alligators were made available for testing in large numbers through the St. Augustine Alligator Farm and Zoological Park in St. Augustine, Florida, U.S.A. The majority of the animals in this facility were hatched from wild-collected eggs, although there are a few large long-term captive nuisance animals that were collected as adults from the wild.

**Force Transducers**

Quantifying the ontogeny of bite-force performance in *A. mississippiensis* required the ability to measure animals ranging from small hatchlings to very large adults. In making comparisons among animals differing so greatly in size, it was necessary to insure that all animals produced kinematically comparable bites that could be measured with precision. To meet these requirements, we used three different bite-force transducers (small, medium, large). A small transducer was employed in the testing of specimens < 90 cm TL (≤ 2 kg). The medium and large transducers were used to measure the bite forces of alligators ranging from 90-200 cm TL (2-50 kg) and > 200 cm TL (> 50 kg), respectively. Bite forces were tested at a homologous location in the jaws among all specimens and to within a few degrees of complete jaw closure.

The basic design of the small transducer is a double-cantilever beam made of stainless steel plates to superficially resemble a tuning fork (see Dechow and Carlson, 1983). Uniaxial foil strain gauges were mounted on the top and bottom surface of each beam (TML Tokyo Sokki Kendyou Co., Ltd., Tokyo, Japan, FLA-3-11-3L) and wired in a full-bridge configuration such that the voltage output was proportional to the compressive force applied to the beams during biting (Fig. 1). Analog signals from the small transducer were amplified (National Instruments Inc., Austin, TX, SCXI Strain Isolation Amplifier), converted to a digital form (National Instruments Inc., PCMCIA-card), and acquired on a laptop computer (Apple Computer, Cupertino, CA; Macintosh G3 Powerbook) at a sampling rate of 1000 Hz using a customized virtual instrument run in LabVIEW 5.1 (National Instruments Inc.).

The small transducer was calibrated by hanging a series of weights from the end of each beam. The mass of each weight and the voltage output for it was recorded and plotted. The transducer produced a nearly perfect
linear relationship, and the slope of this line was calculated for each beam. The slope coefficients were used to calculate the calibration factor (\( [\text{coefficient beam 1}] [\text{coefficient beam 2}] / [\text{coefficient beam 1} + \text{coefficient beam 2}] \)) to convert raw bite-force data into Newtons. The transducer was calibrated before and after a series of bite-force trials and proved to be highly stable. Noise was < 1% of forces generated during actual bites. No data filtering was performed for either the calibrations or bite-force measurements.

The design of the medium and large transducers incorporated piezoelectric load washers sandwiched between 17-4PH stainless steel plates (Fig. 1). The size of animals for which the medium transducer was intended required a thin and narrow design to ensure standardized testing in which only the teeth of interest were engaged. This model had one load washer with a 0-4450 N (1000 lb) range (Kistler Instrument Corp., Amherst, NY, Type 9000M057, \( \leq 1\% \) error, pure DC analog signal with a frequency of display of 10 KHz). The large transducer was designed for use on large alligators with much broader tooth spacing. As such we were afforded the luxury of using a sensor array of four larger load washers (Kistler Instrument Corp., Type 9000M056, \( \leq 1\% \) error, pure DC analog signal with frequency of display of 10 KHz) configured so that a bite anywhere on the steel plates would give a precise force measurement within a range of 0-22250 N (5000 lbs). The piezoelectric transducers were factory assembled, pre-loaded, and calibrated (Kistler Instrument Corp.). Charge output from the transducers was input into a DC-powered charge amplifier (Kistler Instrument Corp., Type 5995) equipped with an LCD display and peak-detect and peak-hold functions, so that maximal bite force could be read at the time of each trial.

<table>
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<th>Transducer Schematic</th>
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**Figure 1.** Designs of the three transducers used to measure bite-force performance in *Alligator*. The general mechanism, measurement range, and size range of animals tested are given for each transducer. Dimensions provided on the transducer schematics are in mm.

**Testing Protocol**

Prior to conducting a bite-force trial, leather pieces were affixed to the working surfaces of a given transducer with the following thicknesses (small transducer: 2.5 mm; medium transducer: 6 mm; large transducer: 6 or 12 mm, depending on size of specimen). The leather pieces served as points of contact for the teeth of the alligators to ensure that the potential for dental trauma from impacting the steel plates was minimized. Leather pieces were removed following each trial to provide a record of the dental contacts made during each bite-force measurement.

For testing, animals were secured by strapping them onto a wooden plank to ensure that axial rolling did not occur, a potential source of signal not related to bite force. If necessary, the animals were encouraged to gape with
taps to the top of the snout. The appropriate transducer then was placed unilaterally between the jaws and centered both mesially and distally at the apex of the 11th the maxillary tooth, the most prominent tooth at the back of the jaws. The sensing of the device upon the teeth typically elicited extremely aggressive, snapping bites. Kinematically, these bites were similar to those used by these animals during prey seizure and during intraspecific aggression in which lateral thrusting of the head leads to unilateral seizure of the quarry (Pooley, 1989; Grenard, 1991; Erickson, 1996b). The shattering of teeth often occurs during such bites in the wild and/or captivity as bones (Erickson, 1996a), wooden handling sticks (personal observations of KAV and GME), metal objects (McHenny, 1935), or occasionally force transducers with insufficient leather cushioning (present study), are encountered. Obviously, an animal’s dentition is only functional within the range of stresses it can sustain, and thus it is very likely the forces we recorded approach the maximum possible for these animals.

During each trial, peak bite force was recorded from the computer (small transducer) or charge amplifier display (medium and large transducers). All trials were digitally videotaped at 30 fps with a Hi-8 digital camcorder (Sony Inc., Tokyo Japan, DCR-TRV520). At least one aggressive, snapping bite was elicited and recorded for each specimen. Post-testing analysis of bite marks on the leather contacts and the videos were used to verify that recorded bites had occurred on the active surface of each transducer, parallel with the jaw line, and directly centered about the 11th maxillary tooth. Trials for which these criteria were not met, for which the bites were not aggressive, or which were discontinuous from start to finish were not utilized in the analyses.

**Morphometrics**

Three measurements of body size were taken after each bite-force trial. Using a tape measure, snout-vent length was measured to the nearest 0.5 cm. Mass was determined to the nearest gram using a spring scale for individuals <10 kg and to the nearest 0.1 kg for larger animals using a platform scale. Total length also was measured to the nearest 0.5 cm. This last measure would be used to relate our results to those of other published research on dietary ecology that used total length as a body size indicator (e.g., Dodson, 1975).

**Statistical Analysis**

Raw bite force data were plotted against snout-vent length and mass. The data then were log-transformed for further analysis. Simple linear regression was done with snout-vent length and mass as the independent variables and bite force as the dependent variable. For each regression, 95% confidence intervals were calculated and plotted using StatVIEW v5 (SAS Institute Inc., Cary, NC) for Windows.

**RESULTS**

Aggressive bite-force readings were obtained from 41 specimens spanning a 12-fold range in snout-vent length and a 3800+-fold range in body mass (Table 1). Peak bite force performance spanned nearly a 800-fold range (12-9452 N; Table 1).

Bite-force performance was significantly and highly correlated with both snout-vent length and mass (Table 2). Bite-force regressions scaled to snout-vent length and body mass gave coefficients departing significantly from the scaling coefficients of 2.0 and 0.66, as predicted by isometric growth, respectively (Fig. 2A, 2B).

**Table 1.** Ranges for raw morphological and bite-force data.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL (cm)</td>
<td>15.5</td>
<td>189.0</td>
</tr>
<tr>
<td>Mass (kg)</td>
<td>0.077</td>
<td>296.7</td>
</tr>
<tr>
<td>Bite Force (N)</td>
<td>12</td>
<td>9452</td>
</tr>
</tbody>
</table>

**Table 2.** Summary of simple regression analysis. BF = bite force.

<table>
<thead>
<tr>
<th>Variables</th>
<th>R²</th>
<th>Intercept</th>
<th>Slope</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL vs. BF</td>
<td>0.972</td>
<td>-1.90</td>
<td>2.59</td>
<td>1337</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mass vs. BF</td>
<td>0.975</td>
<td>-0.31</td>
<td>0.79</td>
<td>1491</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
**Figure 2.** Log-log plots of peak bite-force performance on snout-vent length and mass. Solid lines are the regressions for the data, light dashed lines are 95% confidence bands, and heavy stippled lines show scaling predictions based on isometric growth. (A) Bite force as a function of SVL with predicted scaling coefficient of 2.0. (B) Bite force as a function of body mass with predicted scaling coefficient of 0.66.

**Figure 3.** Plot of TL vs. peak bite-force performance. Vertical lines are placed at the TLs at which major ontogenetic dietary shifts are known to occur, based Dodson’s (1975) review. Note the considerable increase in bite-force performance just beyond 200 cm TL, within the size range reported to include large mammals and turtles as prey. Bite force continues to increase at even larger body size (> 300 cm TL), at which time even larger mammals become part of the diet of *Alligator*.

**DISCUSSION**

This study is the first to accurately and precisely measure bite-force performance throughout ontogeny in a large crocodilian species and demonstrates that such analyses are feasible on all crocodilian taxa. *Alligator*
mississippiensis is one of the largest crocodilian species, and, as such, there is no reason that all crocodilians, including the largest taxon, Crocodylus porosus, could not be tested using the protocol described herein.

Significant changes in the types and physical attributes of prey consumed by A. mississippiensis occur during ontogeny (Kellogg, 1929; McIlhenny, 1935; Giles and Childs, 1949; Fogarty and Albury, 1968; Chabreck, 1971; Valentine et al., 1972; Dodson, 1975). Our preliminary research shows that these dietary shifts are achieved without modification to the continuous allometric trajectory seen throughout life (Fig. 3). In other words, each shift in trophic ecology was not achieved with a discreet increase in bite force compared to the previous growth stage. Instead, an overall disproportionate increase in bite-force performance with size appears to broaden the scope of predatory opportunities for A. mississippiensis so that adult alligators include large prey characterized by rigid integumentary or skeletal elements (e.g., turtles, large mammals).

The incorporation of measures of muscle force generation and lever mechanics with direct measures of bite force and system compliance to create musculo-skeletal models of jaw adduction in A. mississippiensis will be required to evaluate the influence of each of the myriad of factors potentially responsible for the allometric patterns of bite-force performance.

This research illustrates the potential for measuring bite-force performance throughout ontogeny in crocodilian taxa. These data form a vital bridge between morphological variation and realized ecological niches. A comprehensive understanding of the form, function, performance, ecology, and even evolution of crocodilian feeding will be gained from further future investigations of whole-animal performance. Such standardized investigations on crocodilians and other taxa are encouraged.

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Body Condition Factor Analysis for
the American Alligator (*Alligator mississippiensis*)

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**ABSTRACT:** Condition indices have been used to analyze the fitness of animal populations for the last 50 years. However, the indices are complex and can be used inappropriately if unfamiliar with the constraints. For example, condition for crocodilians has been calculated numerous times using Relative K, developed for fisheries in 1952. Relative K is useful for comparing the condition of a population over time, but not appropriate for comparisons among populations.

We analyzed morphometric measurements of the American alligator (*Alligator mississippiensis*) to determine which are measured most accurately and are appropriate for condition analyses. Condition indices are functions of a body length indicator and a volumetric measurement and are only as accurate as the measurement used. Head length, snout-vent length and total length are suitable for body length indicators and tail girth, neck girth, chest girth, and mass can all be used as volumetric measurements. We then compared four condition indices and two models of volume/length relationships for their ability to distinguish between populations with known qualitative condition differences. Condition indices were Fulton’s K, Relative K, a simple length/volume ratio, and relative mass. We also modeled volume/length with a residual index and ANCOVA.
Capturing and Marking American Alligators
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We evaluated passive integrated transponder (PIT), monel web, and cranial mounted reflector tags for marking and identifying American alligators (Alligator mississippiensis). We also tested the use of harmonic radar for relocating marked alligators. A total of 368 adult and 2,674 hatchling alligators were captured between May 1997 and October 1999 using innovative techniques. PIT tags were estimated as 84% reliable on adult and 97% reliable on hatchling alligators during the 3-year study. Placement location and possibly construction characteristics of the tag affected retention of PIT tags. Web tags were estimated to be 92% reliable at 60 days.

Cranial reflectors were unreliable and poorly retained (39% retained) during the 3-year study. PIT tags showed good retention and allowed identification of alligators without visually seeing or handling the animal. Harmonic radar proved of little use in relocating alligators due to short detection ranges (less than 15 m) when tags were at or just below water level.

With increasing attention on alligators and crocodiles, published information on techniques is essential. Additionally, as research needs demand more long-term studies, the needs for tags being of long-life and high reliability increase. Significant variation reported between species, years, and studies preclude reliable extrapolation from studies reporting tag retention rates to alligators (Bjorndal et al. 1996).

Methods of tagging alligators include toe clipping, tail-scute notching, and placement of monel tags. Studies marking American alligators as part of life history research have used the methods of toe clipping and tail-scute notching as originally described by Chabreck (1963). The combination of these 2 marks can provide identification of over 3,000 individuals. Researchers, however, are increasingly marking alligators using individually numbered monel tags placed on webbing located between the toes (Goodwin and Marion 1978, Jacobson and Kushlan 1989, Rootes et al. 1991, Rootes and Chabreck 1993), allowing for an unlimited number of alligators to be marked and later identified.

Our objective was to describe handling techniques and provide an initial evaluation of the use of 3 individual identification tag types (cranial mounted reflectors, monel web tags, and passive integrated transponders) and a harmonic radar relocation system on American alligators.

STUDY AREA

Sabine National Wildlife Refuge is located in southwestern coastal Louisiana. The study area encompassed two impoundments on the refuge and contained vegetative types consistent with fresh (8 km²) and intermediate (21 km²) marsh (Chabreck and Linscombe 1988). The main source of water for the impoundments was rainfall. Dense marshhay cordgrass (Spatina patens) dominated the habitat. Canals bordered the impoundments. The border levees of the impoundments were vegetated with Chinese tallow-tree (Sapinum sebiferum), sea-myrtle (Baccharis halimifolia), and clumps of roseau cane (Phragmites communis). The marsh was interspersed with shallow, open water pools many of which were being colonized by bullwhip (Scirpus californicus) and cattail (Typha spp.). Each unit had at least one public access point used by recreationists and alligator hunters.

METHODS

Alligators of all sizes were targeted for capture. Larger alligators were captured throughout the two impoundments starting during the courtship period (April and May) and continuing through the nesting season (June through September). Hatchling alligators were initially captured near natal nest sites following their hatch
in September. Alligators of, or under, 1.5 m total length were hand-grabbed at the neck. Alligators over 1.5 m were noosed using a cable snare.

A 0.95 cm diameter snare cable noose was attached to a 2.54 cm diameter pole of 3 m length using of a flexible PVC hose of compatible diameter. The noose was attached by swivel to a rope. The rope was passed through the hose and anchored to the boat. The noose was slipped over the head of the alligator and tension applied by the alligator allowed the snare cable to separate from the pole. Alligators were allowed to spin freely until they tired and rotation slowed. As described by McIlhenny (1935), noosed alligators were pulled onto the side of the boat and while applying a forward pulling force on the noose cable, the top jaw was pressed downward against the floor of the boat using a pole or foot. Once closed the mouth was kept shut with approximately 10 size-64 rubber bands. Alligators were pulled to stable locations (i.e., the deck of the boat or flat ground) for processing. Alligators were kept restrained by applying downward pressure to the top of the head and when necessary to the area over the pelvis; eyes were covered with a cloth during processing. Alligators over 3 m total length were restrained on land due to the weight of the animal. During processing tags were applied, body measurements taken, sex identified and notes made of condition and physical abnormalities. The larger alligators were categorized within 4 size classes based on total lengths: Small (1.52-1.82 m), Medium (1.83-2.12 m), Large (2.13-2.42 m), and Very Large (> 2.42 m). Alligators were released at the site of capture and rubber bands removed by pulling an attached cord. Hatchling alligators were placed in a bucket with 8 cm water while awaiting marking. They were restrained with one hand and released on site.

A two person team captured, handled, and marked all alligators. Only animals marked with cranial reflectors were anesthetized.

Alligator dens were checked for the presence of alligators using a 1.27 cm diameter iron pole of 3 m length. The pole was pushed down through the roof systematically until the entire den was searched. The approximate dimensions of each den were recorded. When alligators were found, the pole was used to agitate the alligator with the purpose of causing increased activity (i.e., oxygen consumption); alligators were easily made active by a simple touch. Alligators were noosed when they surfaced to breathe at the den entrance.

In addition to free noosing alligators within marsh pools or out of dens, alligators were captured using baited lines. The baited lines were similar in appearance to that used in Louisiana’s harvest of alligators, but a wooden dowel was used in place of a barbed hook. Approximately 20 cm of nylon seine twine (size 30) was attached to the two ends of a 1.27-cm diameter wooden dowel of 10 cm length. A domestic chicken’s leg was attached with rubber bands to the dowel. The 20-cm piece of twine was attached to enough twine of the same size to reach from an anchor to deepwater habitat (i.e., the middle of a canal or deep pool). Objects not easily uprooted, such as bushes or artificial stakes, were used to anchor the twine. The baited dowel was hung approximately 61 cm above water level using a clothes pin attached to a 3-m pole of 2.54 cm diameter pushed into the ground at a 30-degree angle. Alligators that swallowed a baited dowel were carefully raised toward the water’s surface by pulling the twine up through the noose. Alligators were noosed prior to surfacing with a large diameter snare loop. Once the alligator was noosed, the twine was cut and the alligator restrained as usual.

All alligators were marked with a non-unique tail notch and an uniquely coded Passive Integrated Transponder (PIT) tag. Alligators captured during the 1999 field season and of at least 1.52 m total length, additionally received a web tag. For alligators marked previous to and handled during 1999, a second PIT tag was placed within the left ear flap along with the web tag on the foot. Web tags consisted of an individually numbered self-piercing monel tag (Style 1005-4, National Band and Tag Company, Newport, Kentucky). The tag was placed between the third and fourth toes on the left front foot of alligators. Cranial mounted reflectors were applied to alligators during 1997 only.

The tail notch was created by removing the third single tail scute. The removal of this scute created a distinct gap within the symmetry of the tail and was spotted easily on recapture. This mark (“C” notch) was used as a general identifier of study animals.

Adults were injected with 12 mm x 2 mm (American Veterinary Identification Devices [AVID], Norco, CA) or 11 mm x 2 mm (Destron-Fearing Corp, St. Paul, MN) PIT tags subcutaneously within the right ear flap. Hatchling were injected with 11 mm x 2 mm PIT tags with BioBond (Destron-Fearing Corp, St. Paul, MN) into the right neck with the tag resting subcutaneously above the sternomandibularis muscle. BioBond provided true
anti-migration characteristics to the PIT tag. A Standard Reader and water resistant probe (American Veterinary Identification Devices [AVID], Norco, CA) were used to identify PIT tags.

Only 18 adult alligators received cranial mounted reflectors. The mounting of the cranial reflector was based on descriptions provided by Smith (1972) and Yerbury (1977). This mark was used to identify individual alligators. Anesthetic (tiletamin-zolazepam) was administered previous to tag application (Clyde et al. 1994). A 5 cm by 3.5 cm by 3.5 cm reflector plate was used and consisted of clear epoxy poured around a flat aluminum plate of 0.6 cm thickness with mounted reflector flags. The aluminum extended out of the epoxy resin and served as a point of connection to the skull. The tag was attached to the skull using #8 stainless steel screws. Holes measuring 2.38 mm were drilled through the plate and 5 mm deep into the posterior end of each squamosal bone. A 6 mm space was left under the plate and pre-filled with all-purpose acrylic to prevent necrosis of the skin. The acrylic pad hardened after the attachment was made.

Commercially produced harmonic radar tags (Recco AB, Lidingo, Sweden) measuring 6.5 cm by 2.2 cm by 0.8 cm were placed subdermally under the bony neck scutes of all adult females. This tag was used to locate alligators and numbers etched within the tag’s surface served as a backup identifier of individuals. A 3-cm incision was made posterior to the rear-most neck scute and the tag was inserted through the incision. The tag was pressed forward into place under the leading bony neck scutes. The skin was sealed using tissue glue. The tags were relocated using a hand-held sending/receiving unit (Model RSP1) produced by the same company.

The retention rates of the 3 tags and tail notch were estimated using a binomial distribution and a 0.05 probability level in association with the number retained and functional out of tagged animals reexamined. Percentages used to calculate the mean and 95% Confidence Intervals (95% CI) were transformed to achieve uniform variance using the arcsin of the square root of the estimate. Linear regression was used to describe the detection range for 60 artificially placed harmonic radar tags. Twenty tags were manually placed at each of the following heights compared to water level: -2.54 cm, 2.54 cm, and 91.44 cm. Half of the tags at each of the heights were oriented so to be parallel to the sending/receiver unit; remaining tags were oriented to be perpendicular. The predictor variables included within the model were height of tag compared to water level and orientation of the tag. The response variable was the maximum distance at which the tag was detected.

RESULTS

Individual alligators (2,674 hatchlings and 368 alligators over 1.52 m) were captured between May, 1997 and October, 1999. Alligators over 1.52 m were assumed to be adults. The adult sex ratio for captures was 1 male to 5.24 females. Small, Medium, Large, and Very Large alligators made up 8.5%, 27.1%, 8.5%, and 55.9% of male captures, respectively. Small, Medium, Large, and Very Large alligators made up 5.8%, 22.3%, 43.1%, and 28.8% of female captures, respectively. Average workup time for non-hatchling alligators not receiving a cranial reflector was 14.02 minutes (SE = 0.83). Workup time was significantly longer when cranial reflectors were being applied (F1,312 = 15.50, P = 0.001) and averaged 31.36 minutes (SE = 2.84), excluding time for recovery from anesthesia.

Approximately 31% of males and 54% of females were captured out of dens, and 9% of alligators were captured using baited lines. Most alligators captured at dens (89%) were not seen prior to investigation of the den. Alligators left the den after an average of 36 minutes of agitation (range: 1 - 186 minutes). All agitation times over 60 minutes were at dens where alligators were seen prior to searching the den. Additionally, alligators appeared less likely to leave dens a second time after a failed noose attempt. For 4 alligators agitated within the den, missed, and then re-harassed and captured, the first attempt took an average 15 minutes of harassment and the second attempt took an average 80 additional minutes of agitation. The average dimensions of the 75 dens measured were the same size regardless of the adult’s sex or size class. The average den had a 2.4 m (SD = 1.0) long tunnel that ended in a 0.9 m (SD = 0.2) diameter rear chamber. The longest den tunnel measured was 7 m and the largest diameter chamber recorded was 1.5 m. Tunnels were generally straight and chambers slightly offset to one side of the tunnel. Dens were at least 60 cm underground. All dens examined (n = 232) had only 1 entrance.

No instances of tail-notches being lost were recorded for hatchlings (n = 204) or adults (n = 117). Fifteen (4%) and 101 (27%) adult alligators were naturally missing parts of, or entire, feet and various lengths of tail,