

CROCODILES

8th Meeting

1986

**Special Reprint of the Proceedings of the
8th Working Meeting
of the Crocodile Specialist Group**

**of the Species Survival Commission of
IUCN - The World Conservation Union**

convened at

Quito, Ecuador 13 - 18 October, 1986

(Unedited and Unreviewed)

**IUCN - The World Conservation Union
Rue Mauverneyey 28, CH-1196, Gland, Switzerland**

**Reprinted 2002
by Taxon Media, Inc.
PO Box 192
Lanesboro, MN 55949**

IUCN
The World Conservation Union



SPECIES SURVIVAL COMMISSION

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Originally published by IUCN, Gland, Switzerland and Cambridge, UK
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Copyright © October, 1986, International Union for Conservation of Nature and Natural Resources
 (originally as two volumes)
 © October, 1986, International Union for Conservation of Nature and Natural Resources
 (supplement: Crocodiles Their Management, and Conservation)

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Citation: Author (date). *Title*. IUCN, Gland, Switzerland and Cambridge, UK. xx + xx pp.

ISBN: 1-885209-31-2

Cover design by: Dan Beaver

Cover Photo: F. Wayne King

Available from: Taxon Media
 PO Box 192
 403 Parkway Ave N
 Lanesboro, MN 55409
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**Proceedings of the 8th Working Meeting of the Crocodile Specialist Group
of the Species Survival Commission of the International Union for
Conservation of Nature and Natural Resources convened at**

Quito, Ecuador

13 to 18 October 1986

International Union for Conservation of Nature and Natural Resources

Avenue du Mont Blanc, CH-1196, Gland, Switzerland

1989

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ISBN 2-88032-905-1

Published by: IUCN, Gland, Switzerland.

TABLE OF CONTENTS

| | |
|---|-----|
| FOREWORD | iv |
| SUMMARY OF THE MEETING | v |
| LIST OF PARTICIPANTS..... | xii |
| African and Australasian Reports | |
| Hutton, J.M. Production efficiency at crocodile rearing stations in Zimbabwe..... | 1 |
| Webb, G.J.W. Crocodilian research in the Northern Territory, 1984-86..... | 16 |
| Webb, G.J.W., P.G. Bayliss, and S.C. Manolis. Population research on crocodiles in the Northern Territory, 1984-86..... | 22 |
| North American Reports | |
| Brisbin, I.L., Jr. Radiocesium levels in a population of American alligators: a model for the study of environmental contaminants in free-living crocodilians | 60 |
| Hunt, R.H. Predation of alligator nests in Okefenokee Swamp National Wildlife Refuge, Georgia, U.S.A..... | 74 |
| Joanen, T. and L. McNease. Classification and population status of the American alligator..... | 79 |
| Staton, M. A., I. L. Brisbin, Jr., and G. M. Pesti. Feed formulation for alligators: an overview and initial studies | 84 |
| Tamarack, J.L. Georgia's coastal island alligators: variations in habitat and prey availability | 105 |
| South American Reports | |
| Brazaitis, P. The caiman of the Pantanal: past, present, and future..... | 119 |
| Cintra, R. A comparison of sizes of caiman in hunted and non-hunted areas in the Brazilian Pantanal | 125 |
| King, F.W. and D.H. Videz Roca. The caimans of Bolivia: a preliminary report on a CITES and Centro de Desarrollo Forestal sponsored survey of species distribution and status | 128 |
| Trade, Management, and Conservation Reports | |
| Brisbin, I.L., Jr. and M.A. McDonald. Genetic Patterns and the Conservation of Crocodilians: A Review of Strategies and Options | 156 |
| Gorzula, S., J. Paolini, and J.B. Thorbjarnarson. Applications of Limnology and Hydrology to Crocodilian Conservation and Management..... | 169 |
| Honegger, R. Crocodilian utilization and public education: difficulties in explaining conservation..... | 183 |
| Thomas, A. An overview of crocodile management in Australia 1985-86, with particular reference to the Northern Territory..... | 185 |
| Villalba-Macias, J. S. South American exports of crocodile skins | 200 |
| Villalba-Macias, J. S. Illegal trade in crocodilian skins | 204 |

FOREWORD

This volume is a record of the presentations and discussions that occurred at the 8th Working Meeting of the Crocodile Specialist Group in Quito, Ecuador, 13 to 18 October 1986. Its publication was supported by contributions from Professor Harry Messel and the University Foundation for Physics, University of Sydney, Australia; the Griffis Wildlife Conservation Fund of the University of Florida Foundation, Gainesville, U.S.A.; and Jacques Lewkowicz of Société Nouvelle France Croco, Paris. The opinions expressed herein are those of the individuals identified and are not the opinions of the International Union for Conservation of Nature and Natural Resources or its Species Survival Commission. Phil Hall was scientific and managing editor, Rhoda Bryant was copy and style editor.

The International Union for Conservation of Nature and Natural Resources (IUCN) was founded in 1948, and has its headquarters in Gland, Switzerland; it is an independent international body whose membership comprises states, irrespective of their political and social systems, government departments, and private institutions as well as international organizations. It represents those who are concerned at man's modification of the natural environment through the rapidity of urban and industrial development and the excessive exploitation of the earth's natural resources, upon which rest the foundations of his survival. IUCN's main purpose is to promote or support action which will ensure the perpetuation of wild nature and natural resources on a world-wide basis, not only for their intrinsic cultural or scientific values but also for the long-term economic and social welfare of mankind.

This objective can be achieved through active conservation programs for the wise use of natural resources in areas where the flora and fauna are of particular importance and where the landscape is especially beautiful or striking, or of historical, cultural, or scientific significance. IUCN believes that its aims can be achieved most effectively by international effort in cooperation with other international agencies, such as UNESCO, FAO, and UNEP, and international organizations, such as World Wild Fund for Nature (WWF).

The mission of IUCN's Species Survival Commission (SSC) is to prevent the extinction of species, subspecies, and discrete populations of fauna and flora, thereby maintaining the genetic diversity of living resources of the planet. To carry out its mission, the SSC relies on a network of over 2,000 volunteer professionals working through 100 Specialist Groups and a large number of affiliate organizations, regional representatives, and consultants, scattered through nearly every country in the world.

SUMMARY OF THE MEETING

The 8th Working Meeting of the IUCN/SSC Crocodile Specialist Group (CSG) was convened in Quito, Ecuador, from 13 to 18 October 1986. The meeting was hosted by the Pontificia Universidad del Ecuador and the Fundación Natura, and would not have been possible without the tireless efforts of Drs. Eduardo and Ana Cristina Asanza who handled local arrangements, and numerous university students who assisted with registration and operated the audiovisual equipment used during the sessions.

The meeting was open to anyone actively involved in crocodilian conservation or farming. More than 60 participants registered for the meeting and delivered a total of 48 papers and audiovisual presentations on the status of crocodilian populations, management problems and successes, legal and illegal trade, and the latest research developments; 17 of the papers were submitted for publication and appear below (see Table of Contents).

Dr. Julio Terán Dutari, Rector of the Pontificia Universidad Católica del Ecuador, opened the meeting at the university and welcomed the participants. Additional welcoming comments were delivered by Sr. Manuel Kakabadse, Director of the Dirección Nacional Forestal, Ministerio de la Agricultura y Ganadería; Dr. Tjitte de Vries, Director of the university's Department of Biology; Sr. Roque Sevilla, President of the Fundación Natura; and Dr. Luis Romo, President of the Comunidad Científica Ecuatoriana.

Following two days of sessions, the participants traveled by plane and boat to Limoncoche where two days were spent observing the *Melanosuchus* and *Caiman* population being studied by Eduardo Asanza. The final working session, the business meeting, was held on the Orellana floating hotel during the return trip to Quito. A summary of the business session deliberations follows.

PUBLICATIONS

Publication of Commercial Volume on Crocodile Biology and Conservation. Although the CSG members had agreed to contribute to a commercial volume on crocodilians at the 1984 working meeting, and a number had signed agreements with the publisher, 60% of the chapters still had not been submitted despite the deadline having passed months ago. The chairman indicated that the chapters that had been turned in would be returned to the authors or compiled into a special volume to be published in the IUCN series on crocodiles.

CSG Newsletter. The members commended the format and currency of the Newsletter, and recommended that Peter Brazaitis and Myrna Watanabe continue to serve as editors. To ease the work load, Lehr Brisbin was asked to serve as assistant editor for business matters.

Catalogue of American Amphibians and Reptiles. The chairman, who had just become the editor of the crocodilian accounts in the Catalogue of American Amphibians and Reptiles published by the Society for the Study of Amphibians and Reptiles, asked if any people present were working on accounts. Records from the previous editor were incomplete and do not indicate who has been asked to write accounts. Several members indicated they were writing accounts and provided a list of prior assignments.

FUNDRAISING FOR CSG OPERATIONS

The cost of CSG operations such as publication of the Newsletter, postage and telephone expenses, and travel has been borne by the chairman's and editor's offices, however, assistance is needed. In addition there are other costs not presently being covered, such as travel assistance for getting students and members from tropical nations to meetings, and funding for special projects. Following some discussion the members agreed that, provided the Group's ethical standards remained high and uncompromised, it was appropriate to ask the international hide trade to contribute to support of the CSG. It was recommended that a fundraising committee be appointed.

RECOMMENDATIONS TO THE CITES SECRETARIAT

Transfer of Nile Crocodile Populations from CITES Appendix I to Appendix II under an Annual Quota. The members were unanimous in opposing transfer of any crocodile populations from Appendix I to Appendix II without supporting data to justify the transfer. Support was expressed for removal of quotas from any nation that, by the time of the 1989 CITES Meeting of the Conference of the Parties, has not developed the management and monitoring programs promised at the Buenos Aires meeting. However, the CSG also recognized the need to assist nations in developing and implementing monitoring and ranching programs to replace the quotas. John Hutton pointed out that wildlife officials in many African nations do not know what data are needed to justify downlisting of crocodile populations or how to generate the data. As a remedy, John Hutton drafted a,

PROJECT FOR THE ASSISTANCE OF SADCC MEMBER STATES WITH CROCODILE MANAGEMENT AND UTILIZATION

Introduction

The Nile crocodile, *Crocodylus niloticus*, occurs in suitable habitat throughout the SADCC (Southern Africa Development Cooperation Conference) region and frequently comes into conflict with legitimate human interests. Extensive human fatalities have been reported from Malawi, Mozambique, and Zimbabwe. The level of this conflict is increasing which reflects, at least in part, the recovery of crocodile populations from over-exploitation in the 1950s. In several SADCC countries crocodiles are now sufficiently numerous to be a valuable natural resource promoting conservation.

For 20 years Zimbabwe's wild crocodiles have supported such a harvest. Eggs collected from the wild, hatched and the young crocodiles raised for their skins. In 1985 this industry earned approximately U.S. \$1,000,000.00, all in foreign exchange, and provided a conspicuous incentive for the conservation of wild crocodile populations. The success of this policy resulted in Zimbabwe's crocodiles being downlisted from "endangered" under CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), allowing unrestricted trade. A similar, largely untapped potential for crocodile utilization exists in neighboring states.

Five other SADCC countries (Botswana, Malawi, Mozambique, Tanzania, and Zambia) have, either through SADCC or the CITES forum, indicated that they intend to undertake crocodile utilization. In 1984 an "African proposal" was presented to the 5th Meeting of the Conference of the Parties to CITES by Malawi, supported by 25 other African countries and a consultancy report, asking that the status of the crocodile be moved from Appendix I (Endangered) to Appendix II (Threatened) - the prerequisite for utilization. Only certain populations were downlisted and an export quota system was adopted. Botswana did not request a quota at the time (it has since done so by postal vote) but the other SADCC countries received quotas as follows at the CITES meeting in Buenos Aires: Malawi (500), Mozambique (1,000), Tanzania (1,000), and Zambia (2,000).

Quotas are due to be reviewed in April 1987 and supporting data will be required. Member countries have few resources to dedicate to submissions of the type required for downlisting of species by the CITES Parties, and a second round of quotas is anticipated. This shortage of resources requires that SADCC states wishing to initiate sustainable crocodile utilization be assisted in some or all of the following areas:

- a. Pre-feasibility studies (harvesting potential of wild populations, production options);
- b. Policy and legislation (adaptation of legislative and institutional frameworks to allow efficient and controlled utilization);

- c. Feasibility studies (identification of potential production sites, evaluation and quantification of the factors inherent in utilization, production plans and a working document);
- d. International requirements for trade (the research and drafting of CITES submissions, documentation and tagging);
- e. Census and monitoring (technical advice for the derivation of simple and appropriate schemes, training of local manpower);
- f. Technical aspects of crocodile propagation in captivity (planning, extension, management training); and
- g. Marketing.

Programme

The programme is divided into two parts:

1. Feasibility, policy and preliminary surveys (a,b,c, and d above).
2. Implementation - technical assistance with captive propagation, census and monitoring and marketing (e,f, and g above).

The first part of the programme is designed to give each country a clear indication of its options, a policy for utilization, a plan for its implementation and an unequivocal document for submission to CITES before April 1987.

The second stage is intended to transfer technical skills within the SADCC region to result in a coordinated regional production and marketing system which is efficient and sustainable, together with a system of monitoring.

Programme details

1. Feasibility, policy and preliminary surveys.

As a general principal, egg collection and "farming" will yield more skins than cropping of wild crocodiles, but this advantage can be offset by the expense of such factors as food supply or initial capital investment. The choice of a utilization strategy requires a detailed investigation of both crocodile abundance (exploitation potential) and propagation potential. Following this, farm sites, the availability (and economics) of the supply of food and water, the suitability of the environment and the availability of management skills will be assessed.

It is neither simple nor inexpensive to census crocodile populations, but the problems must be faced. In the "African proposal" only Mozambique and Zimbabwe submitted recent census data and that for Mozambique was inadequate to allow discrimination between the utilization options. In this part of the programme preliminary surveys will be carried out using any existing database, critical localities will be identified and the requirement for census and monitoring under Part 2 assessed.

Assistance will be given in the formulation of a clear Government policy on crocodile management and on the required institutional framework. Private involvement in exploitation usually necessitates controlling legislation. Government involvement may require the establishment of a managing body with responsibility for revolving funds, foreign exchange matters

and the training of management and other manpower. The required safeguards will be built into the policy.

Based on the recommended magnitude of exploitation, preliminary utilization plans will, at this stage, allow economic assessment and prediction.

When Government is satisfied that it has identified a management scheme suited to its aspirations, the correct submissions and undertakings will be made to ensure problem-free international trade. Preliminary marketing suggestions will be made.

2. Implementation.

The technical input required in implementation will vary between countries depending on existing skills and management policy. It is envisaged that detailed structural and management plans will be provided where private enterprise is not extensively involved. Even where private investment is paramount, Governments will initially find it advantageous to provide extension services of the kind found in Zimbabwe. Experience has shown that even with good facilities, the success of crocodile utilization depends on the quality of management. Management training will be provided within the SADCC region.

In almost all circumstances the necessary surveying and monitoring will strain fully committed wildlife budgets. The rapid identification of census priorities in Part 1 will be followed up by detailed surveys to provide baseline data and correction factors on which subsequent simple, inexpensive monitoring will be based. Local skills will be created as appropriate.

The expertise required in this programme is available within SADCC, principally within Zimbabwe.

John Hutton also prepared a budget for this proposal, but it is not included here.*

Transfer of the Botswana Nile Crocodile Population from CITES Appendix I to Appendix II under an Annual Quota. The CSG submitted to the CITES Secretariat a lengthy critique of the report Botswana submitted in support of its postal petition for transferring its Nile crocodile population to Appendix II under an annual quota, which the CITES Secretariat summarized and transmitted to the CITES Parties as:

"The Group will oppose the proposal until the Government of Botswana certifies to the CITES Parties that:

- a) it has limited and will continue to limit the exploitation of the Okavango crocodiles to the collection of wild eggs and hatchlings;
- b) it has and will continue to ban the exploitation of wild crocodiles over 2 meters in length, except for problem crocodiles that threaten humans and livestock;
- c) by protecting from all exploitation geographically widespread populations in national parks and wildlife reserves, it will conserve the biotic diversity of the Botswana crocodiles at a level that will allow them to perform their natural function in the ecosystem;
- d) it will establish a programme for monitoring (censusing) the status of crocodile populations similar to the programmes of Zimbabwe and Papua New Guinea; and

* Following the CSG meeting this proposal was funded by World Wildlife Fund U.S.A. and a meeting of wildlife officials from SADCC nations was convened in Harare, Zimbabwe, under John Hutton's leadership prior to the July 1987 Meeting of the Conference of the Parties to CITES in Ottawa, Canada.

e) it will implement a marking system for legal crocodile hides and products, ...

If these things would be agreed and implemented by the Government of Botswana, then the CSG could support the modified proposal."

Prior to notifying the Parties, the Secretariat transmitted the CSG comments to the Botswana authorities, who responded with additional information on items a) and b) above. However, they indicated no plans to develop monitoring or hide tagging programs, items d) and e) respectively. After considering the comments of the various Parties, the CSG, and the Government of Botswana, the CITES Secretariat recommended that the Parties support the petition. As a consequence the postal vote probably will approve Botswana's petition.

Report on the Conservation of the Indonesian Saltwater Crocodile Population. The Indonesian population of *Crocodylus porosus* was transferred from Appendix I to Appendix II at the 1985 CITES conference in Buenos Aires. A copy of an Indonesian government report on the program for conserving the saltwater crocodile in Irian Jaya was received from the CITES Secretariat. There was too little time to translate the report into English before the CSG meeting, so the full content of the report was not available for review and discussion by the Group. A translation is expected to be available during 1987.

FARMING AND RANCHING

Interest in farming and ranching crocodilians continues to grow worldwide. The CSG supports the development of these establishments, but captive production of crocodilian hides and meat does not replace the need to conserve the species in the wild. As stated in Article IV(3) of CITES governing trade in Appendix II species, efforts should be made to "... maintain that species throughout its range at a level consistent with its role in the ecosystems in which it occurs" In order to accomplish that, wild populations that are subject to harvest must be rigorously managed to avoid over exploitation, and populations throughout the range of the species should be totally protected in national parks and wildlife sanctuaries in order to preserve genetic diversity.

Cameroon. Richard Luxmoore reported on a preliminary proposal to ranch crocodiles in Cameroon and indicated that he would keep the CSG informed as the project developed.

Philippines. Unconfirmed reports concerning attempts by the Republic of the Philippines-Japan Crocodile Farming Institute to obtain *Crocodylus novaeguineae* for stocking its farm in Puerto Princessa, Palawan Island, were reviewed. It was decided that letters would be sent to appropriate authorities in the Philippines expressing the CSG's concern over the possibility of escaped farm stock resulting in the establishment of an exotic species of crocodile into the Philippines. In addition, Victor Onions will visit the Palawan farm within the next two months and will report back to the CSG.

Honduras. The chairman reported on *Crocodylus acutus* farms being established in Honduras. The main farm is being developed by a cattle rancher and slaughter house operator, but a study commissioned by World Bank is expected to advocate additional farms.

Bolivia. The chairman reported on efforts to develop *Caiman yacare* farms in Bolivia. Bolivian law requires all caiman hide tanners to operate farms to lessen the pressure on the wild population from the export of 50,000 or more hides. None of the tanner's farms were anything more than natural ponds and lakes with no supplemental feeding or other intensive management. However, one of the tanners is planning to establish a caiman farm that would utilize the offal from a nearby slaughter house. In addition, one true farm operated by a heavy equipment importer apparently already exists.

Colombia. A farm for *Caiman crocodilus* has been developed by Monterrey Forestal in Sambrano, Colombia. Reportedly additional farms have been established in other parts of the country, but details are lacking.

CESSATION OF BARRAMUNDI NETTING IN THE RIVERS OF KAKADU NATIONAL PARK. The CSG received a letter from the head of the Australia's federal national park service reporting that the decision had been made to close all the rivers in Kakadu National Park to barramundi netting. The closure will be phased in over a period of months. The Group decided that in the light of IUCN General Assembly Resolution 16/26 Conservation of the Australian population of the saltwater crocodile (*Crocodylus porosus*), the chairman should write to appropriate government officials in Australia to congratulate them on the closure.

TAGGING OF HIDES IN INTERNATIONAL TRADE. Greg Mitchell indicated that all hides moving in international commerce should be tagged with locking, tamper-proof tags, like the ones used by Papua New Guinea, the U.S.A., and Zimbabwe to identify legal hide exports. The universal use of tags on legal hides would be an immense aid in regulating international trade. Following the discussion, the CSG approved a resolution on tagging:

WHEREAS, the importance of affixing tamper-proof tags to legal commercial crocodilian hides to distinguish them from illegal hides is widely recognized, and

WHEREAS, several countries have successfully implemented hide tagging programs; and

WHEREAS, data (such as number of crocodilians harvested annually, skin size, trade routes, and countries of origin) generated by a hide tagging program are of great utility to proper management of wild crocodilian populations.

NOW THEREFORE BE IT RESOLVED, that the Crocodile Specialist Group assembled on the occasion of its 8th Working Meeting in Quito, Ecuador, 13-18 October 1986, recommends that a universal tagging system, involving tamper-proof, serially numbered tags inscribed with country of origin, be implemented worldwide, and

BE IT FURTHER RESOLVED that countries of origin establish a monitoring program in order to maintain permanent records of all tags issued, especially with respect to size class of crocodilians harvested.

CSG ACTION PROGRAM FOR CROCODILIANS. Professor Messel reported on the need to produce an action program for crocodilian conservation in which the projects are priority ranked. At the last meeting the Group agreed to produce such a program for the SSC, but most members had not submitted regional or national projects to the chairman for inclusion in the overall program. Following further discussion, the CSG members renewed their commitment to produce an action program.

INTERNATIONAL ALLIGATOR AND CROCODILE TRADE STUDY (IACS). Ted Joanen asked the Group to endorse a continuation of the IACS study. During the sessions on the second day of the meeting in Quito, Don Ashley had introduced the people who compiled the three parts of the study of international trade in classic alligator and crocodile belly hides; Ginette Hemley of TRAFFIC U.S.A., and Richard Luxmoore of the IUCN Conservation Monitoring Centre, Cambridge, U.K., and Tom Milliken of TRAFFIC Japan. Each of these individuals presented their portion of the study, but the papers were not submitted for publication in this volume. The CSG gave a vote of confidence to the authors of the three studies and agreed by resolution that the IACS survey should be continued.

WHEREAS, the International Alligator and Crocodile Trade Study (IACS) has produced valuable data on international trade in classic alligator and crocodile belly hides; and

WHEREAS, the data produced by IACS is useful for management of crocodilian populations; and

WHEREAS, the U.S. Fish and Wildlife Service, the Louisiana Department of Wildlife and Fisheries, the Florida Game and Fresh Water Fish Commission, and the Texas Parks and Wildlife Department provided financial support of the IACS.

NOW THEREFORE BE IT RESOLVED, that the Crocodile Specialist Group on the occasion of its 8th Working Meeting in Quito, Ecuador, 13-18 October 1986, recommends a

continuation of the study and of its support by the various alligator producing states and the U.S. Fish and Wildlife Service.

INTERNATIONAL CONGRESS OF HERPETOLOGY. Rene Honegger described plans for the 1st International Congress of Herpetology in 1989, and indicated that CSG members should participate. He and Romulus Whitaker are on the organizing committee. Topics relevant to the CSG are on the agenda of the congress.

The first part of the paper discusses the importance of the research and the objectives of the study. It then proceeds to a literature review, highlighting the key findings of previous studies in this field. The methodology section describes the research design, data collection methods, and the statistical analysis used. The results section presents the findings of the study, and the discussion section interprets these findings in the context of the research objectives. Finally, the conclusion summarizes the main points of the paper and suggests areas for future research.

The research was conducted in a systematic and rigorous manner, following the principles of good research practice. The data was collected from a representative sample of the population, and the analysis was conducted using appropriate statistical techniques. The results of the study are presented in a clear and concise manner, and the discussion provides a thorough interpretation of these results. The conclusion of the paper is based on the findings of the study and provides a clear summary of the main points.

The study has several strengths, including a large sample size, a rigorous methodology, and a clear focus on the research objectives. However, there are also some limitations to the study, such as the potential for bias in the sample and the limitations of the statistical analysis. These limitations are discussed in the paper, and the authors suggest ways to address them in future research.

The paper is well-structured and easy to read, with a clear flow of ideas and a logical progression of the argument. The language is clear and concise, and the writing is of a high standard. The paper is a valuable contribution to the field and provides a clear and concise summary of the research findings.

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PRODUCTION EFFICIENCY AT CROCODILE REARING STATIONS IN ZIMBABWE

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INTRODUCTION

Zimbabwe recognizes wildlife as a renewable resource and believes that conservation is encouraged when the resource is used for the benefit of the people who live with it (Child 1977, 1987). This philosophy is illustrated by the sustained-yield utilization of the Nile crocodile (*Crocodylus niloticus*) in which, for 20 years, crocodile eggs have been collected from the wild and hatched, and the hatchlings raised for their skins on licensed rearing stations (Blake 1974, 1982; Blake and Loveridge 1975, Shwedick 1979, Child 1987).

This exploitation is controlled by the Department of National Parks and Wild Life Management (the Department) to which stations are obliged to submit monthly stock returns plus cards and maps which record egg collection data.

Similar captive propagation, based on the exploitation of wild eggs or hatchlings, is being or has been tried elsewhere and is commonly recommended as a conservation strategy for developing countries (e.g., Medem 1981, Hollands 1987, Whitaker et al. 1985). However, Magnusson (1984) made a number of observations pertinent to the farming and ranching of crocodilians and concluded that, particularly for species with poorly valued hide, captive propagation is unlikely to be as economically viable as controlled hunting.

A strong argument can be made to the effect that rearing is usually preferable to hunting where a species has a classic hide (Hutton and Child submitted ms.), but this largely depends on estimates of the efficiency that can be achieved in captive propagation. Figures commonly quoted for the success of hatching and rearing of crocodiles in Zimbabwe are drawn from a preliminary analysis, made in 1975, of each rearing station's returns (Blake and Loveridge 1975). This paper updates Blake and Loveridge (1975) and reports on the production and efficiency (percentage of fertile eggs resulting in saleable hides) of Zimbabwe's crocodile rearing stations from the inception of return forms until August 1986.

METHODS

Zimbabwe has five well established crocodile rearing stations: Kariba Crocodile Farm (Kariba) established 1965, Binga Crocodile Farm (Binga) established 1967, Spencer's Creek Crocodile Ranch (Spencer's Creek) established 1971, Sengwa Crocodile Ranch (Senga Mouth) established 1977 and Rokari Crocodile Ranch (Rokari) established 1981. Each of these is currently producing hides from a mixture of farming and ranching. Stations are allocated permits to collect eggs from crocodiles which are otherwise fully protected throughout Zimbabwe (Hutton 1986). Permits carry a number of standard conditions including the requirement that stations keep a stock register and from this make a monthly return to the Department. After egg collection and hatching, they also submit egg record cards and maps showing the locality of each nest. Stock returns are available, in one form or another, since 1965; records of egg collection since 1971 (Appendix 1).

The data in these records were extracted to give information on hatching and subsequent rearing success. As an index of the care with which each station compiled returns (prior to 1985) a comparison was made of the total number of crocodiles which hatched according to their egg record cards and monthly stock returns.

The Department, in terms of Zimbabwe's commitment to CITES, is required to issue a special permit giving details of the size, value and origin of each export consignment of crocodiles and their products. These permits, together with monthly stock returns, were used to provide information on the number of hides being produced by each station.

RESULTS

a. Information from return forms.

Monthly return forms were standardized in 1978 (Appendix 1). Before this they varied greatly in the amount of information they contained. Those from Binga allow accurate assessment of hatchling mortality from 1968, whereas similar information can only be extracted from Kariba after 1978.

Prior to 1985 the difference between the number of hatchlings recorded on egg cards and monthly returns was consistently below 1% at Kariba, Binga and Rokari, but large (up to 15%) and variable at Spencer's Creek and Sengwa Mouth (there should have been no difference). Spencer's Creek and Kariba commonly returned a large percentage of incomplete egg cards (up to 29%) while, by contrast, those from Sengwa Mouth were always complete (Hutton and Brennan 1985).

b. Number of wild eggs collected and discarded.

At present, only the crocodile population of the Zambezi Valley is exploited. Eggs are collected from three sub-populations, that of the upper Zambezi River and its tributaries west of Lake Kariba, that of Lake Kariba and its inflowing rivers and that of the lower Zambezi River downstream (east) of Kariba dam. Prior to 1985 the quota of wild eggs given to any station never exceeded 2500 and was commonly less (Fig. 1). The total number of eggs removed from the wild rose sharply in 1977 and 1981 when the two most recent stations were opened. In 1985 almost 14000 eggs were collected from approximately 300 nests. The majority of these eggs (82%) were collected from Lake Kariba (Fig. 2).

By tradition, only good eggs have counted against quotas and because eggs which appeared inviable were discarded, the total number of eggs handled was greater than that collected for incubation. Between 1982 and 1985 the percentage of eggs discarded by some stations rose to almost 20% (Fig. 3) while the mean rejection rate was 14.5%. The system has now been changed so that all eggs count against quotas which have been increased by 10% to compensate (10% is the mean inviability rate at Lake Ngezi, Zimbabwe [Hutton 1984]). In 1985, the first year of the new system, the mean rate of rejection fell to 7.4%, but mean incubation success remained high (88.8% in 1984 and 90.5% in 1985).

c. Eggs from captive stock.

Kariba has been collecting eggs from captive breeding stock since 1974, Spencer's Creek since 1976 and in 1985 all five stations obtained eggs in this way (Table 1). It is notable that in 1984 Spencer's Creek obtained 2185 eggs from captive breeding stock and only 711 from the wild population.

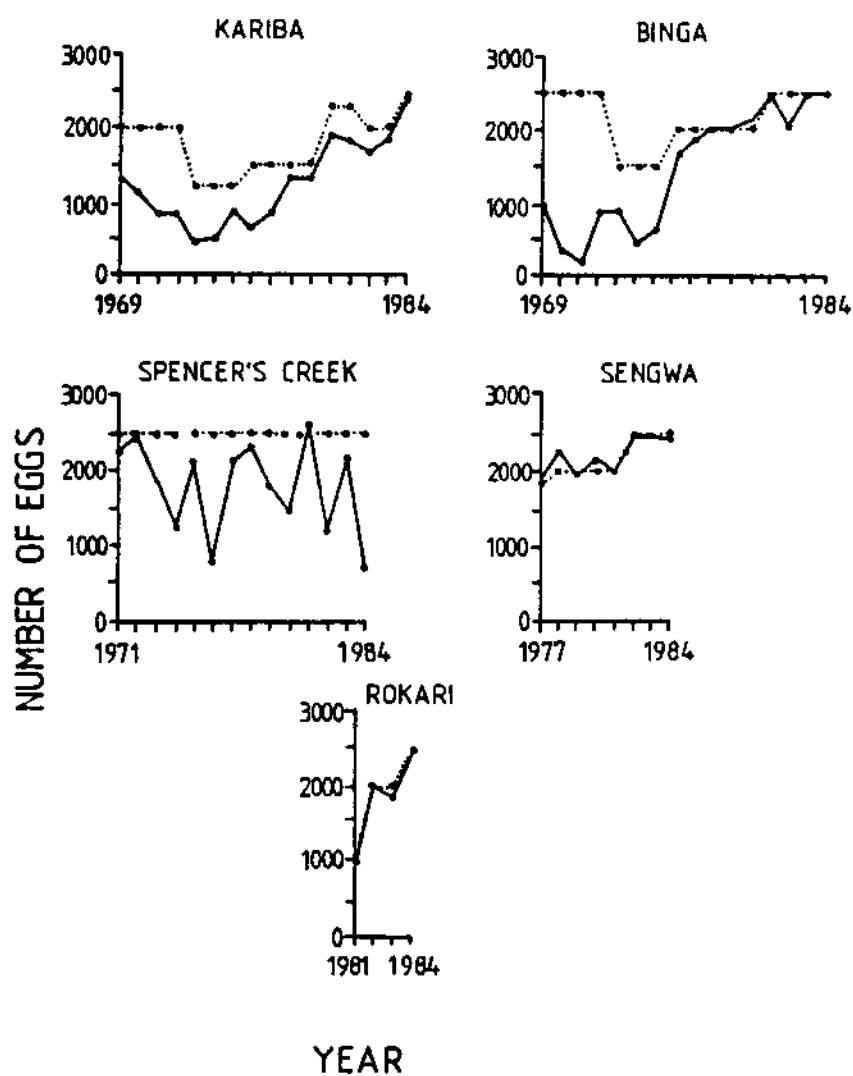


Figure 1. The quota of wild eggs allocated to each station (●-●-●-●-●) and the number of viable eggs collected (●-●-●-●-●), 1969-1984.

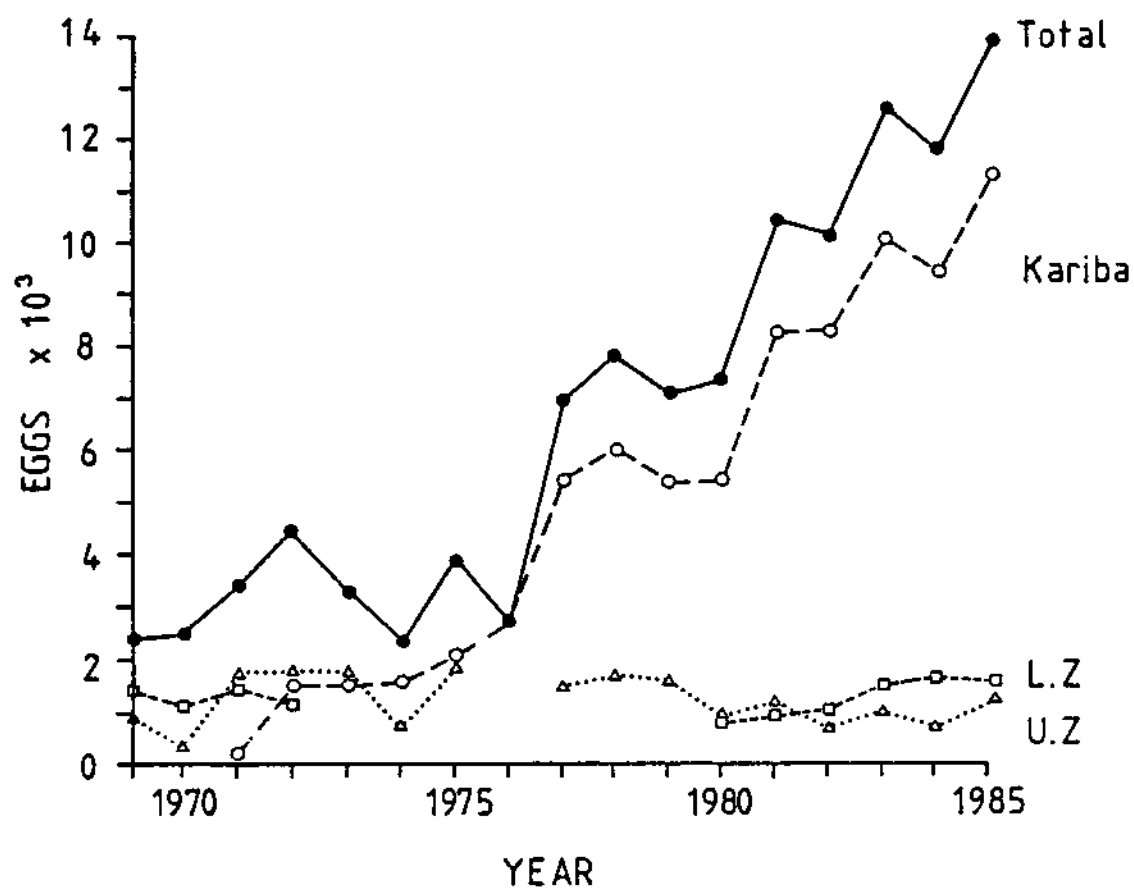


Figure 2. The total number of eggs removed from nests in each of the three main collecting areas of the Zambezi Valley since the first issue of egg collecting permits. U.Z. = Upper Zambezi River; L.Z. = Lower Zambezi River; Kariba = Lake Kariba.

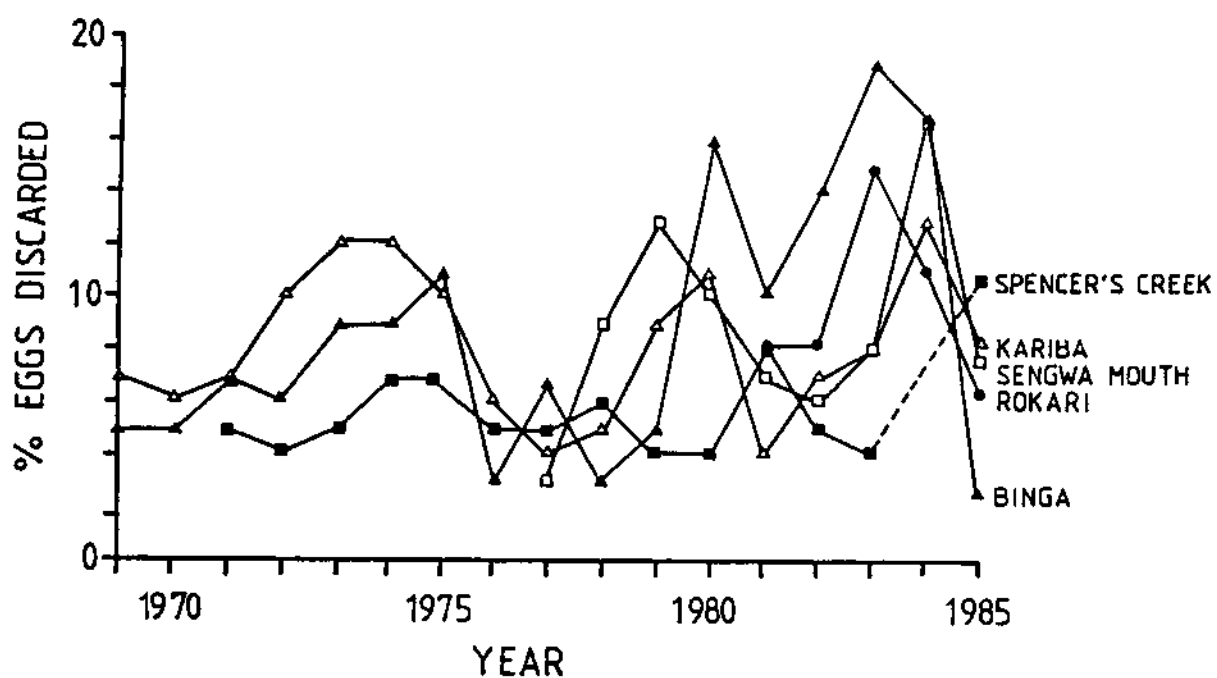


Figure 3. The percentage of eggs discarded by the collectors of each station, 1969-1985.

d. Hatching success.

Generally, since 1979, rearing stations have achieved 80-90% success when hatching wild eggs (Fig. 4). The average over the period 1981-1985 was 89%. At Kariba (where most breeders are F_2) the hatching success from captive stock has been significantly lower than that of wild eggs, but this has not been the case at Spencer's Creek where most breeders have been taken from the wild (Wilcoxon matched pairs signed-rank test, $T = 2.5$; $n = 9$; $p < 0.005$, and $T = 15.5$; $n = 9$; $p > 0.005$, respectively).

e. Rearing success.

i. Hatchlings - The quantity and quality of crocodiles surviving to the end of their first year has shown great variation both within and between stations. Mortality on the most successful station (Binga) has ranged from 5-55% in consecutive years while, prior to 1986, Spencer's Creek had losses consistently greater than 30% and even suffered a total die-off in 1983. However, since 1983 four stations have achieved losses below 20%, and three are continually improving (Fig. 5). The average mortality of all stations combined during the period 1981-1985 was 28.2%. In the first 8 months of 1986 hatchling losses have been less than 8% on all stations except Kariba where it has been inordinately high (33%). At Spencer's Creek there has been a spectacular reversal of the trend with only 51 of 3314 hatchlings (1.5%) having died.

It is notable that mortality is seasonally variable. A larger percentage of the remaining hatchlings die in September, at the end of the cool season, then in February prior to the cool season or November when the next hot season is advanced (Fig. 6).

ii. Rearing stock - On four stations mortality of rearing stock (yearlings and older) has been commonly below 5% per annum. At Spencer's Creek, however, it has been as high as amongst hatchlings (Fig. 7). The overall mean mortality in the period 1981- 1985 was 3.3%.

f. Hide production

The proportion of viable eggs resulting in saleable hides has varied greatly between stations and on some it has been consistently low. During the two year period 1983-1984 the four established stations exported 6192 hides and a further 696 live animals of cropping size. Binga produced 43% of the total and only Binga and Spencer's Creek managed to harvest 1000 crocodiles each year (Table 2.). As some 8000 fertile eggs were available to stations in each of the years 1978-1982 only about 43% were actually hatched and raised to cropping size. In 1985, 4972 hides were exported. As an average of approximately 9000 viable eggs were collected in each of the years 1980-1983, efficiency had risen to about 54%.

DISCUSSION

The information submitted by some stations has been considerably better than that from others. Simple tests of "reliability" show that records from Binga and Rokari have always been reliable and those from Kariba were reliable after 1979, while those of Sengwa Mouth and Spencer's Creek were difficult to interpret before 1985. As a result of this analysis, record-keeping is being more strictly controlled. In addition, egg cards have been simplified: they were long and tedious to use in the field and much of their information was of dubious value. The accurate marking of nest sites on maps is important for management and has been introduced. When only viable eggs were counted against quotas there was an

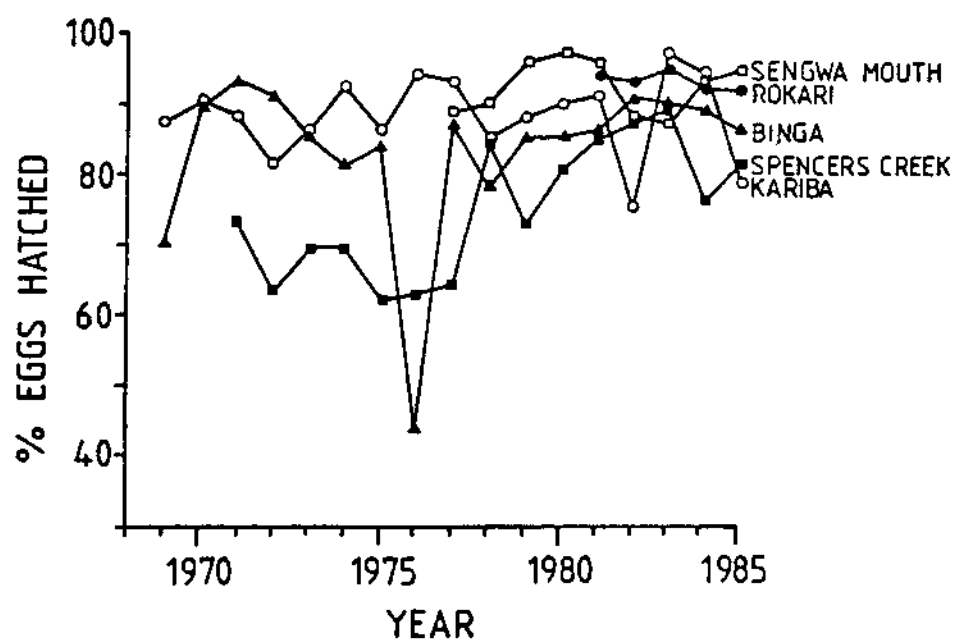


Figure 4. Hatching success of wild eggs on each of the five rearing stations.

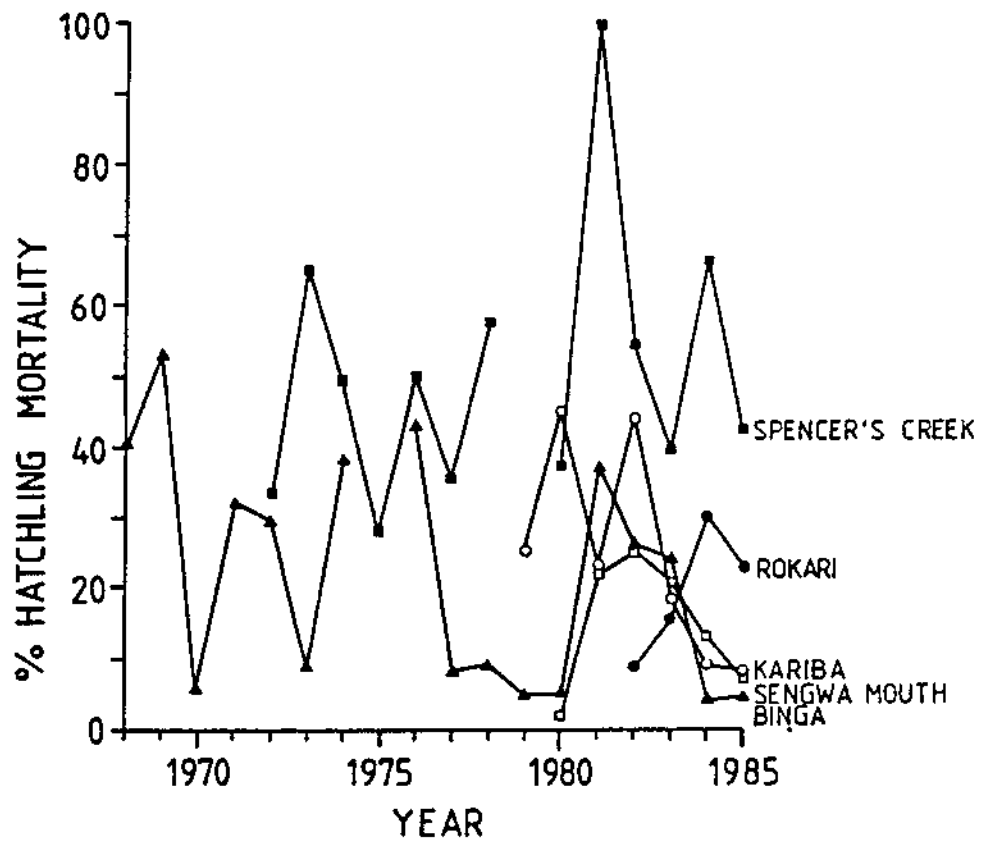


Figure 5. Annual percentage hatchling mortality on each station.

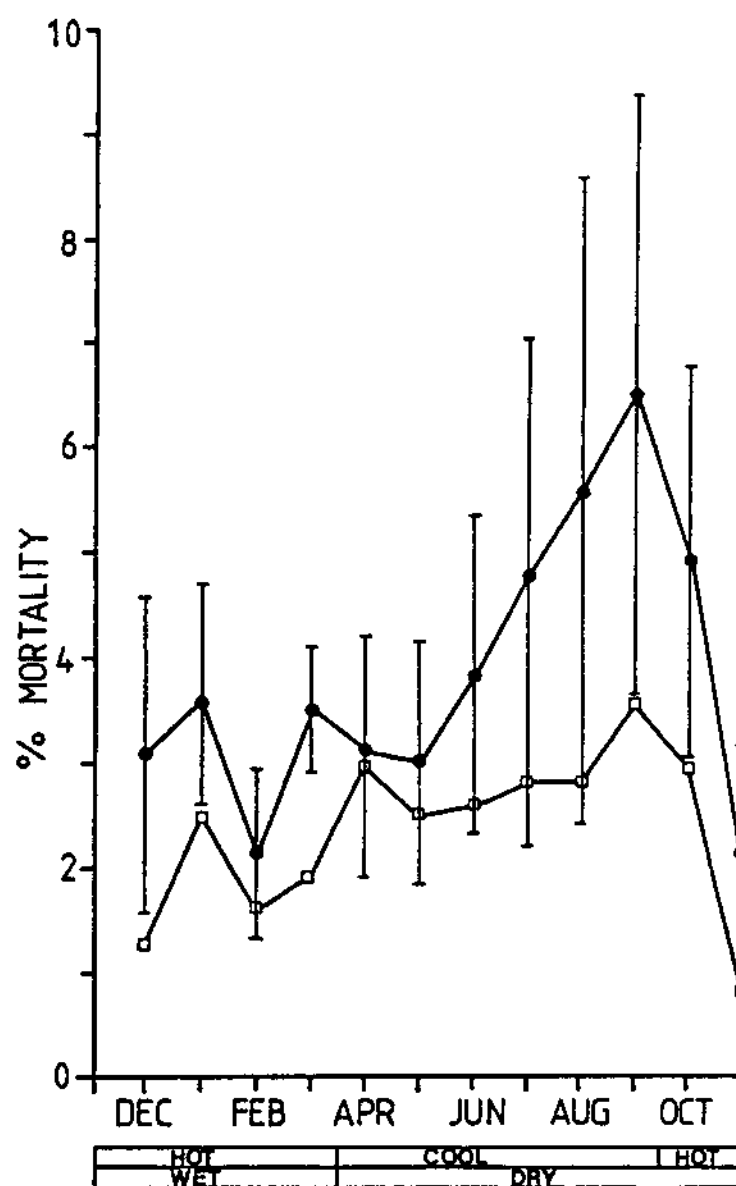


Figure 6. Mean monthly mortality among hatchlings from 1969 to 1984; data from all stations combined (●—●) and with Spencer's Creek omitted (□—□). Vertical bars = 95% confidence interval.

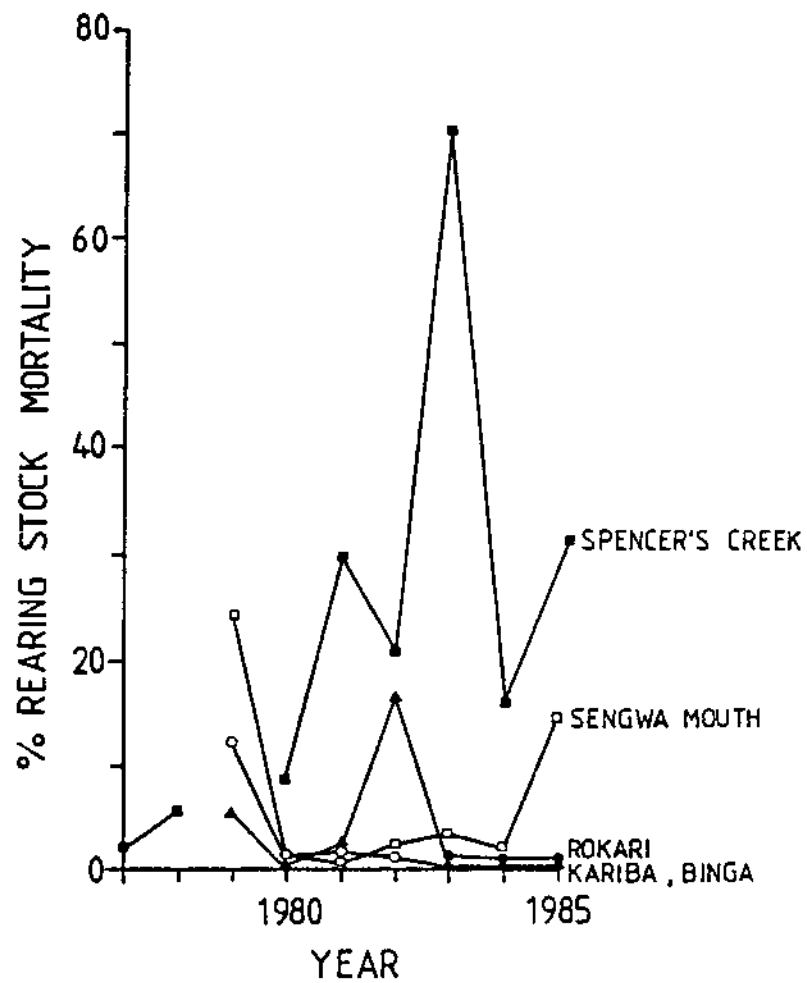


Figure 7. Annual percentage rearing stock mortality on each station.

incentive to discard eggs, the viability of which was uncertain. Inefficiency, therefore, may have been introduced at this earliest stage of the rearing process. As noted, the overall rate of rejection of eggs fell from 14.5% to 7.4% in the first year that the new quota system was introduced, and it is hoped that this improvement will be sustained.

The current overall quota of 14000 wild eggs is likely to continue until there are better data on the size and dynamics of the Zambezi Valley crocodile population. However, the number of captive breeding stock is steadily increasing. Approximately 300 females have been "put aside" and are due to breed in the next five years. Although it is unlikely that all of these will be selected for breeding, Spencer's Creek already produces over 2000 eggs while each of the other stations has the potential to produce 1000 eggs from captive stock. It is therefore not inconceivable that within five years all stations will be producing 2000 of their own eggs.

Blake (1974, 1982) has described egg collection and a similar system continues, though aircraft are increasingly used to find nests. Eggs are usually collected after 50 days because, though never vigorously tested, it appears that collection in the first few weeks after laying causes inordinately high embryonic mortality. However, the time of collection will also affect efficiency if, as suggested, incubation strongly influences the subsequent growth of hatchlings (Hutton 1987; Joanen et al. 1987). Early collection and subsequent controlled incubation is favored, but difficult to achieve in the wild. While eggs are spending 75% of their incubation under natural conditions it is unlikely that hatching success better than 90% can be regularly achieved. The early collection and controlled incubation of eggs from captive stock is being encouraged. It is too early to say if any station has mastered the successful raising of hatchlings, but the low mortality recorded on some stations in recent years is encouraging.

The ultimate cause of death is generally disease (Foggin 1987) and as there is a considerable variation in its occurrence and severity, depending on climate, management, egg incubation, diet and housing, it is clear that these factors play a major role in its development and that severe losses are a manifestation of poor husbandry. As noted, mortality is seasonal, being at its greatest at the end of the cool season (Fig. 6) and the inordinately high loss of animals at Spencer's Creek has generally been attributed to the station's altitude which, at 900 m, is in the frost zone. The exceptional success of Spencer's Creek in 1986 is undoubtedly due to the construction of heated pens for hatchlings and a change in management which resulted in greatly improved husbandry.

Whatever the predetermining factors, disease has seriously affected the viability of crocodile farming in Zimbabwe and largely accounts for the fact that efficiency has been less than 50%. In addition to the economic considerations, there are ethical objections to a system of conservation and management in which large numbers of animals succumb to disease (Foggin 1987).

Cursory examination is enough to show that the variation in success between stations is more related to personality than technology (though there is scope for technical improvement) and that efficiency has been unnecessarily low on some stations. In order to improve the industry's performance, in 1985 the Department and the Crocodile Farmers Association together adopted minimum standards for each stage of the rearing process and any station which does not achieve these may suffer a reduction in its quota of wild eggs. Blake and Loveridge (1975) indicated that the efficiency of the rearing process was inversely proportional to the number of eggs collected and it must be noted that stations encountering serious rearing problems have usually requested reduced quotas for themselves.

According to the minimum standards it is acceptable to have a hatching failure of 15% of fertile eggs, 25% hatchling mortality and 5% mortality of yearlings and older. In fact, with a heightened appreciation of the importance to hatchlings of consistently high temperatures, together with improved technology in this field, it is expected that hatchling losses will fall below 10% while there seems to be no need for rearing stock mortality to exceed 1%.

From losses in the first 8 months of 1986 it is clear that four of the five stations are already set to achieve this expected efficiency. Kariba, which has lost more than 30% of its hatchlings, has experienced atypical conditions and, in any case, has recently been sold to the operator of Rokari.

In conclusion, with recent improvements in management and small changes in technology it is not unreasonable to expect the wild harvest of 14000 eggs to produce an annual crop of 9500 hides at an efficiency of 75%.

ACKNOWLEDGEMENTS

I thank Ranger Technician S. Brennan for assistance with the tedious work of extracting data and the Crocodile Farmers Association for making it possible for me to present this analysis of its members performance.

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APPENDIX 1

Return of Records from Crocodile Rearing Stations

Permits issued to stations between 1965 and 1970 required them to submit monthly returns to the Director of the Department containing: (a) number (with date and place) of eggs taken or crocodiles captured, (b) the number of crocodiles which had died, and (c) number of crocodiles slaughtered, divided into three size classes.

In 1969, "Crocodile Egg Record" cards were introduced to be completed, on a voluntary basis, at the time of collection. These cards record a number of physical characteristics (e.g. the depth of the first egg, distance of the nest from water, the number of fertile and infertile eggs) and also the success of incubation. In 1971, a clause was added to permits requiring that these cards be kept in respect of all nests from which eggs were collected.

After 1969, the collection of live animals was no longer permitted and the permit format was altered. Holders were required to submit, by the 15th of each month, a return in respect of the preceding month giving details of: a) number of eggs collected, b) number of eggs hatched, c) number of crocodiles slaughtered or sold in either age or size classes, d) other adjustments to numbers (escape, etc.).

In June 1978, Form 245 "Return of Reptiles" was introduced and subsequent monthly returns were made on this. These forms recorded the number of hatchlings, rearing and breeding stock, the number which died or were cropped and the number of eggs collected and hatched. Reference to monthly returns was dropped from permits, and from 1978-1984 their conditions read:

- "a) In respect of any nest from which crocodile eggs are collected, a "Crocodile Egg Record" card will be kept.
- b) The holder of this permit shall submit, within 30 days of the expiry of this permit, the following information in respect of eggs removed:
 - (i) the number of eggs removed each month,
 - (ii) number of crocodiles hatched from eggs removed,
 - (iii) completed egg cards."

Crocodiles were divided into age classes, defined as: a) hatchlings: from hatching to one year, b) rearing stock: one year and over, stock being reared for skins, c) breeding stock: animals retained for display and egg production. These definitions have been retained. Hatchlings are transferred to rearing stock in December each year, shortly before new eggs hatch.

In 1982, Form 245 was replaced with the "Form of Register and Return of Amphibia and Reptiles" which must be kept on the rearing station at all times. The top copy is returned to the Department each month.

Table 1. Number of eggs produced by captive breeding stock on Zimbabwe crocodile rearing stations.

| | Year | | | | | | | | | | | |
|-----------------|------|------|------|------|------|------|------|------|------|------|------|------|
| | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 |
| Kariba | 21 | 28 | 416 | 603 | 429 | 581 | 565 | 310 | 602 | 505 | 375 | 534 |
| Binga | | | | | | | | | | | 249 | 619 |
| Spencer's Creek | | | 558 | 535 | 1199 | 1341 | 1499 | 1895 | 1790 | 1729 | 2185 | 2123 |
| Sengwa mouth | | | | | | | | | | 76 | 580 | 611 |
| Rokari | | | | | | | | | | | | 213 |

Table 2. Number of hides and live crocodiles exported between 1 January 1983 and 31 December 1984.

| Station | No. skins exported | No. live rearing stock | Total no. cropped & exported | Yearly mean export |
|-----------------|-----------------------|------------------------------|------------------------------------|-----------------------|
| Kariba | 1002 | 200 | 1202 | 601 |
| Binga | 2781 | 206 | 2987 | 1494 |
| Spencer's Creek | 322 | 270 | 592 | 296 |
| Sengwa mouth | 2087 | 20 | 2107 | 1054 |
| Grand Total | | | 6888 | 3445 |

CROCODILIAN RESEARCH IN THE NORTHERN TERRITORY, 1984-86

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A significant research effort into crocodilians has been undertaken in the Northern Territory of Australia over the period 1984-1986. It has involved collaboration between the Conservation Commission of the Northern Territory and the staff and students of a number of Universities. Highlights are summarized below:

1. EMBRYOLOGY

Research into crocodilian embryology was undertaken in order to improve the success with which crocodilian eggs could be incubated and to increase the "fitness" of hatchlings produced through artificial incubation.

i. Descriptive Embryology

Mark Ferguson's (1985) comprehensive review of crocodilian embryology combined data on *Crocodylus porosus* and *C. johnstoni* embryology obtained in the Northern Territory with detailed information on *Alligator mississippiensis* obtained in Louisiana (also see Ferguson 1987). Techniques for retrieving crocodilian embryos from eggs have been described by Webb and Manolis (1987). Heaphy (1986) examined and described the cutaneous papillae and a series of dorsal organs in the skin of *C. johnstoni* and *C. porosus* embryos and hatchlings.

ii. Egg Function

Yolk rotation, opaque banding and the fluid changes which take place within crocodilian eggs have been linked together in a model of crocodilian egg function (Webb et al. 1987b, c). The effects of rotating crocodilian eggs have also been examined (Webb et al. 1987c). Prior to opaque banding eggs can be rotated without increasing mortality (the yolk will rotate within the egg, bringing the embryo back to the top) and after about 18 days incubation at 30°C they can also be rotated without increasing mortality (the enlarging allantois floats up through the yolk and can still act as a respiratory organ).

iii. Egg Chemistry

The first detailed analysis of the chemistry of crocodilian eggs was undertaken (Manolis et al. 1987). There now exists a large body of baseline information which can be used to determine whether or not deficiencies in the chemistry of captive laid eggs occur.

iv. Embryonic Metabolism

Detailed studies of the metabolic rates and respiratory physiology of *C. johnstoni* eggs and to a lesser extent *C. porosus* eggs have been undertaken by Whitehead (1987a, b). These provide guidelines for the selection of artificial incubation regimes.

v. Embryonic Development Rate

The relationship between embryonic development rate, total incubation time and incubation temperature has been quantified for *C. johnstoni* and *C. porosus* (Webb et al. 1987a).

vi. Sex Determination

Embryonic development rate has been shown to be more closely associated with sex determination than is incubation temperature per se. With both *C. porosus* and *C. johnstoni*, the relationship between incubation environment and sex determination has been quantified, and a series of switch experiments with both species have quantified the embryonic stages at which sex is influenced by temperature. With *C. johnstoni*, increasing incubation temperature within the first four days is sufficient to effect the sex of offspring (Webb et al. 1987a). Research into the histology of the developing gonad is underway at the University of N.S.W. (Michel Beal), and the histochemistry is now being researched at Macquarie University (Jean Joss, America Cuff). The development of the pituitary, which appears to be involved in sex determination, is being studied at the University of New England (Martin Dillon).

vii. Effects of Incubation Environment

The relationship between hatchling size and the amount of residual yolk hatchlings contain is a function of embryonic development rate. Fast development (high incubation temperatures) gives small hatchlings with abundant residual yolk - slow development gives the reverse (Webb et al. 1987a). Preliminary results from studies currently underway indicate that post-hatching survivorship and growth in *C. porosus* and *C. johnstoni* are both partly dependent on incubation conditions, as has been demonstrated for *A. mississippiensis* by Ted Joanen. A method for estimating the amount of residual yolk from the dimensions of a hatchling's abdomen has been described (Smith and Webb 1986).

viii. Theoretical Explanation for Temperature

With post-hatching growth and sex each being influenced by incubation temperature (or rate of embryonic development), the sex determining mechanism could function to ensure maleness was only allocated to embryos endowed with the potential for fast growth and large size within the egg. This hypothesis would predict the opposite relationship between incubation temperature and sex in turtles, where females are usually bigger than males, which in fact occurs.

2. ECOLOGY AND NATURAL HISTORY

I. Reviews

Comprehensive reviews of the ecology and population dynamics of *C. porosus* and *C. johnstoni* were prepared as supporting data for the management plans for both species (CCNT 1986a, b).

ii. Sex Ratio and Survivorship in *C. johnstoni*

Anthony Smith is currently completing his PhD (Australian National University) on the sex ratios and survival of recruits within the wild population in the McKinlay River area.

iii. Population Dynamics of *C. johnstoni* in Katherine Gorge

Harvey Stockwell is into the second year of her study of the *C. johnstoni* population in Katherine Gorge and the results to date indicate greatly reduced growth rates, reduced adult sizes and reduced recruitment in comparison to the *C. johnstoni* population in the McKinlay River area.

iv. Population Models

The dynamics of the McKinlay River population of *C. johnstoni* were incorporated into a computer simulation model (Smith and Webb 1985), and sensitivity tests were carried out to identify the priorities that should be given to the measurement of different variables. Survivorship estimates, classically the hardest to measure, are the ones that most effort should be concentrated on.

v. A Standardized Approach to Studying Crocodilian Populations

With the benefits of hindsight, Webb and Smith (1987) examined an approach to studying crocodilian natural history and population dynamics that would maximize the management information obtained. They recognised three levels of resolution that should be addressed from the very start of a study: 1. Rate of increase - is the population stable, increasing or decreasing; 2. A concise summary of life history processes which allows estimates of fecundity, survival by age and size, dispersal, sex ratio and at least some of the sources of variation in each; 3. Compensatory population mechanisms such as density-dependence.

3. HUSBANDRY AND FARMING

I. Parasitology

In collaboration with the Northern Territory Department of Primary Production, a major effort has been expended in isolating and identifying parasites in captive and wild *C. johnstoni* and *C. porosus*.

ii. Husbandry Research

A major husbandry research program is being initiated by the CCNT with intensive raising facilities and a full-time veterinarian to liaise with the crocodile farms. A solar water heating system was tested during 1986 as a means of providing *C. porosus* hatchlings with warm water, but without exorbitant electricity charges. Survivorship among *C. porosus* hatchlings increased as a consequence.

4. C. POROSUS EGG HARVEST

As part of the program to ranch *C. porosus* through an egg harvest program, a major study of *C. porosus* nesting was undertaken in both the 1984-85 and 1985-86 seasons. The results of this study, combined with data already in existence, will allow quantification of time of nesting, the extent of mortality in the field, and the economics involved in collecting eggs from the field. Economic assessments to date indicate that the cost of hatchlings produced from wild collected eggs will be about half that of those produced in captivity. The impact of egg harvests to date appears negligible (Webb et al. 1986).

5. PHYSIOLOGICAL EFFECTS OF CAPTURE

Some large crocodiles caught in the wild have died immediately after capture, and it was considered possible that such deaths could be the result of extreme exhaustion. A study of the effects of capture on blood chemistry was carried out with the imported expertise of Al Bennett (University of California), Roger Seymour and Dave Bradford (University of Adelaide), and it confirmed that extreme respiratory acidosis arose in large crocodilians that had been struggling (Bennett et al. 1985, Seymour et al. 1985, 1986).

6. HABITATS

Floating mats of vegetation, upon which *C. porosus* nest, are beginning to consolidate now that buffalo numbers are being reduced. An additional factor in some areas has been the spread of *Mimosa pigra* (Hill et al. 1987).

7. MONITORING RESEARCH

The University of Sydney have carried out spotlight surveys in the southern Gulf of Carpentaria (Messel et al. 1986) and the Victoria River (Messel, unpubl. data). Monitoring research carried out by CCNT is discussed in more depth by Webb et al. (1987a), Bayliss et al. (1986), Bayliss (1987) and Choquenot and Webb (1987). The main areas of study have been:

- i. Quantifying rates of population increase;
- ii. Obtaining habitat specific correction factors for relating relative density indices to absolute densities;
- iii. Developing helicopter surveys as an alternative to spotlight surveys;
- iv. Obtaining a correction for nest counts to total population size;

- v. Developing a more accurate means of estimating crocodilian sizes in spotlight counts;
- vi. Continuation of the long-term monitoring of some Arnhem Land Rivers.
- vii. of the impact of harvesting.

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POPULATION RESEARCH ON CROCODILES IN THE NORTHERN TERRITORY, 1984-86

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Within the Northern Territory of Australia, *Crocodylus johnstoni* (the Australian freshwater crocodile) and/or *Crocodylus porosus* (the estuarine or saltwater crocodile) occupy most if not all coastal wetlands, regardless of whether they contain fresh or saline water, or are under tidal influence or not (CCNT 1986a, b). The wetland habitats range from open coastline to densely vegetated swamps, from long meandering tidal rivers with exposed mudbanks to perennial streams in rocky escarpments and scattered flood plain billabongs. The extent of all wetlands is strongly influenced by season - particularly by flooding during the wet season.

The diverse habitats occupied by crocodiles in the Northern Territory make quantification of the distribution and abundance of both species difficult. Survey methods need to be habitat specific, and the numbers of animals or nests counted using different methods may need to be standardized against each other, or corrected to real numbers (absolute densities), depending on the management problems being addressed. Where the proportion of large crocodiles in the population is changing as recovery continues, a new set of variables needs to be accounted for; the visibility of large and small crocodiles is not necessarily the same due to size itself and to size-related effects of wariness (Bayliss et al. 1986).

This paper summarizes the results of a series of investigations aimed broadly at refining survey methodology, and clarifying the relationship between relative densities and absolute densities, particularly with *C. porosus*. It addresses Messel's (1986) criticisms of our 1984 estimate of the *C. porosus* population (Webb et al. 1984) and quantifies the rates of population growth that have occurred since the mid-1970's in various habitats. Preliminary data on the impact of harvesting *C. porosus* eggs from the wild are presented.

HABITATS

Habitats occupied by *C. porosus* and *C. johnstoni* in the Northern Territory are summarized on Fig. 1. The majority of *C. porosus* are either in tidal rivers containing saline water during the dry season (B, C, D), or in coastal flood plain channels, billabongs and swamps (E, F, G, H), most of which contain freshwater throughout the year. Wetlands upstream of these, including river channels in rocky escarpments (I) or on upstream flood plains (J), which often recede to chains of billabongs during the dry season, contain mainly *C. johnstoni*. The two species overlap in many river systems giving recognizable zones of sympatry.

The abundance of *C. porosus* habitats in the Northern Territory was estimated on a regional basis (Fig. 2) from 1:100,000 maps supplemented with aerial photographs and information from helicopter and light aircraft surveys (Webb et al. 1984). A distinction was made between tidal rivers where *C. porosus* were known to breed regularly (major breeding) and those where breeding was unknown or irregular (minor breeding). A distinction was also made between mainstreams, secondary creeks (represented by double lines on the maps and generally less than 100 m wide) and tertiary creeks (represented by single lines on the maps and up to 2 km long).

Notwithstanding the errors involved in any such assessment of habitat availability, the results vary significantly from those used as the basis of a *C. porosus* total population estimate by Messel et al. (1981)

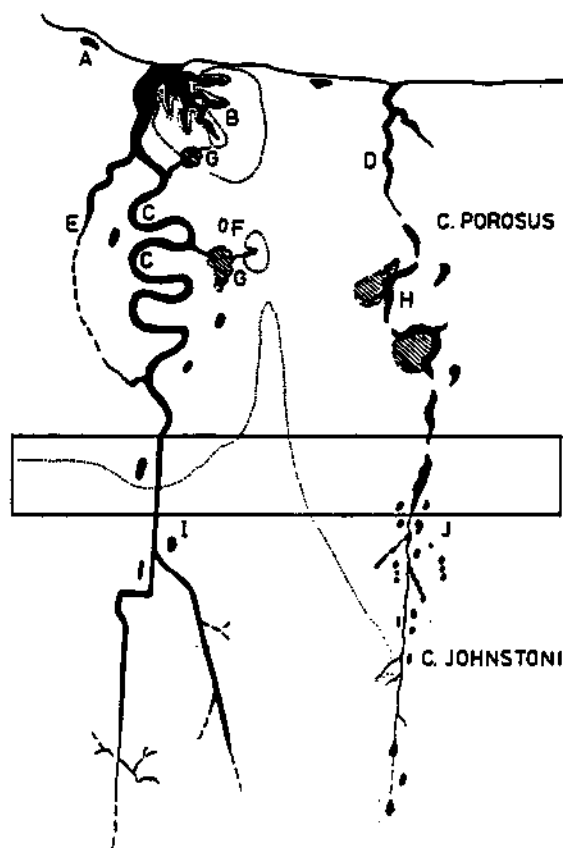


Figure 1. Schematic representation of Northern Territory wetlands occupied by crocodiles. Dotted lines indicate elevated land and cross-hatched lines are freshwater swamps. A, freshwater billabongs behind beach lines; B, a tidal river penetrating into elevated land; C, a tidal river meandering over a flood plain; D, remnant of a meandering tidal river that has become silted; E, tidal flood plain creek with no freshwater input during the dry season; F, isolated flood plain billabongs; G, spring-fed freshwater swamp adjacent to a tidal river; H, isolated sections of an old meandering river no longer open to the sea and containing fresh water and often floating rafts of vegetation; I, non-tidal upper reaches of a river draining rocky escarpment; J, a seasonally flowing mainstream channel that has numerous freshwater billabongs associated with it (after Webb et al. 1987).

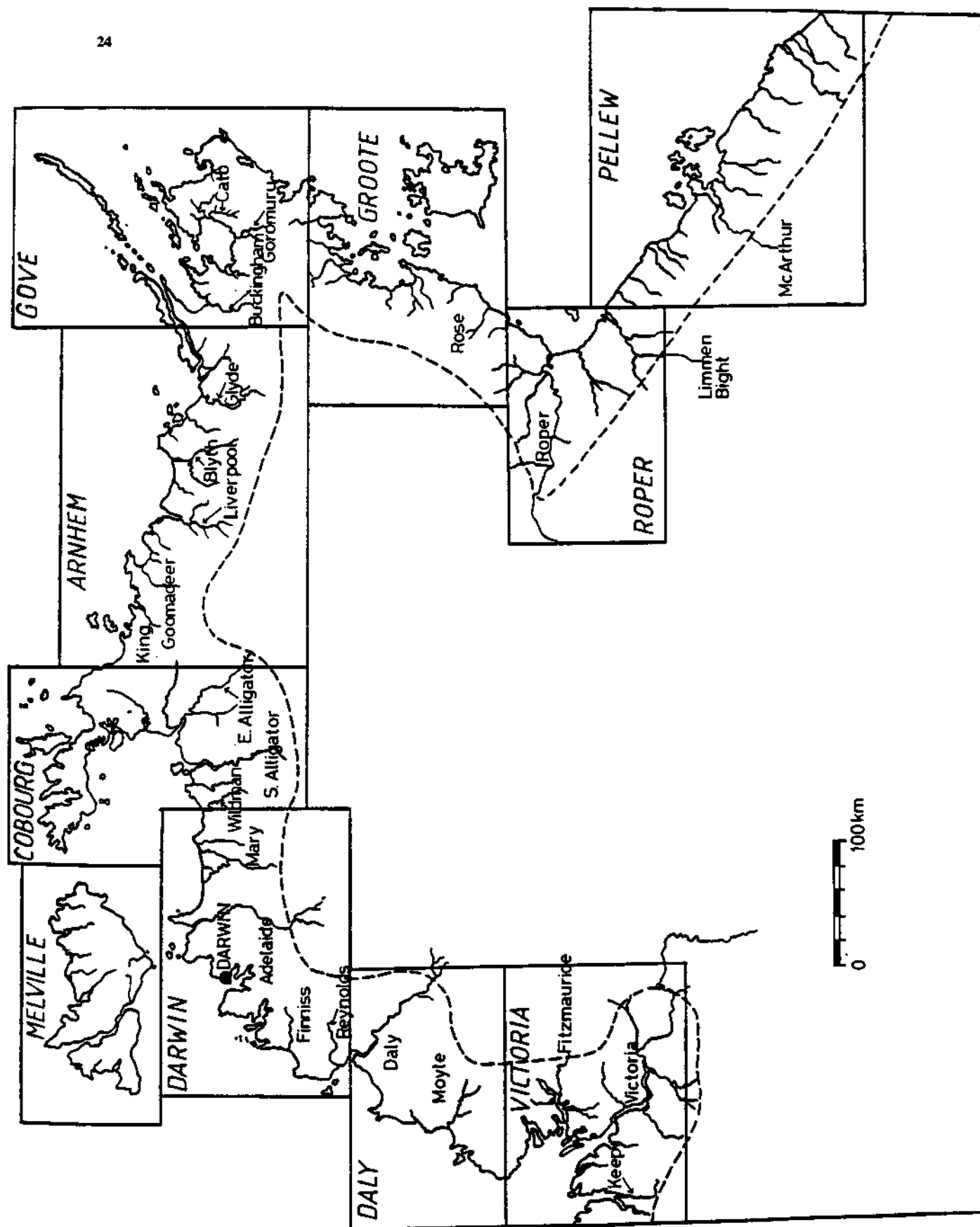


Figure 2. Geographic regions in the Northern Territory in which habitats and population densities have been assessed. The inland limit of *Crocodylus porosus* is indicated by the dashed line.

Table 1. Habitat available for *Crocodylus porosus* in the Northern Territory. C = coastline; C-S = coastal secondary creeks; Mi = minor breeding tiday mainstreams; Mi-S = secondary creeks off minor breeding tidal mainstreams; Ma = major breeding tidal mainstreams; Ma-S = secondary creeks off major breeding tidal mainstreams; TC = tertiary tidal creeks; EC = escarpment channels; FC = flood plain channels; FSw = freshwater swamp.

| Region | C km | C-S km | Mi km | Mi-S km | Ma km | Ma-S km | TC No. | EC km | FC km | FSw km ² |
|----------|---------|-----------|----------|------------|----------|------------|-----------|----------|----------|------------------------|
| Victoria | 435 | 64 | 949 | 205 | - | - | 1487 | 169 | - | 13 |
| Daly | 233 | 28 | 64 | 31 | 110 | 2 | 146 | 51 | 144 | 1401 |
| Darwin | 722 | 122 | 233 | 110 | 230 | 67 | 1425 | 20 | 575 | 392 |
| Melville | 683 | 228 | 380 | 428 | 14 | 1 | 1158 | - | 46 | 67 |
| Cobourg | 1137 | 127 | 224 | 69 | 329 | 38 | 1213 | - | 224 | 826 |
| Arnhem | 666 | 56 | 233 | 57 | 350 | 64 | 502 | 64 | 247 | 793 |
| Gove | 1933 | 299 | 142 | 109 | 181 | 155 | 1090 | 12 | - | 61 |
| Groote | 1563 | 190 | 13 | 4 | 81 | 25 | 431 | 152 | 45 | 145 |
| Roper | 175 | 26 | 242 | 35 | 292 | 53 | 406 | 44 | 10 | 42 |
| Pellw | 725 | 98 | 705 | 92 | - | - | 365 | 22 | - | 33 |
| Totals | 8272 | 1238 | 3185 | 1140 | 1587 | 405 | 8223 | 534 | 1291 | 3773 |

and Messel (1986; Table 2). They did not specifically estimate the amount of freshwater swamp or flood plain channel, but recognised it as *C. porosus* habitat and guessed that the population there was 20% of the their estimated tidal population.

As can be seen from Table 1, the regions on Figure 2 have vastly different proportions of different habitat types. Some regions have extensive breeding habitat and little non-breeding habitat, whereas others have the reverse. These differences are summarized on Tables 3 and 4.

In the Victoria and Pellew regions, where the mean annual rainfall is the lowest in the coastal fringe (Fig. 3), there is minimal breeding habitat for *C. porosus*. These areas never contained high densities of *C. porosus* in the past (Webb et al. 1984), and cannot be expected to do so in the future. The suggestion that over 100,000 *C. porosus* were taken from the Victoria River alone (Messel et al. 1984) cannot be substantiated - the total harvest of *C. porosus* skins from the Northern Territory, during the period 1945-46 to 1971, was about 113,000, and a relatively small proportion of these came from the Victoria River (Webb et al. 1984).

"ALL CROCODILES" VERSUS "NON-HATCHLINGS" IN POPULATION ESTIMATES

The extent to which "young-of-the-year" should be included or excluded from survey data pertaining to crocodilian populations depends on the extent to which they can be recognised in surveys, the level of mortality being experienced at the time of survey, and the population statistic being addressed (total population size or rates of recovery).

With *C. johnstoni*, hatching occurs in a six-week pulse at the start of the wet season (November-December), and mortality is approximately 88% during the first year (Smith and Webb 1985). But this occurs almost exclusively during the first wet season, with some 50% mortality within the first two months (Smith, unpubl. data).

By the following dry season, when spotlight surveys are conducted, "young-of-the-year" are an integral part of the population age structure (Fig. 4). Their probability of surviving is the same as that of older sub-adults (Webb and Smith 1984; Smith and Webb 1985), and in spotlight counts (which are often carried out from a vantage point on the edge of a billabong) they cannot be recognised. There is no logical reason to exclude them from estimates of the total population size based on dry season surveys, nor from analyses of rates of recovery.

With *C. porosus*, hatching occurs from March to September, and peaks in April-May. Most spotlight surveys are conducted between June and November of the same year (in the dry season), when hatchlings are mostly 3-4 months of age, but can range from 0 to 9 months of age. In the Blyth-Cadell River System, 81% of the number of "young-of-the-year" estimated from dry season spotlight surveys were represented as 1 year olds the following year. They have higher probabilities of surviving than do older sub-adult year classes (Table 5). Deleting them from estimates of the total population size on the basis of "low survivorship" is simply not supported by the data. They are a significant but highly variable segment of the population and at least the mean number of hatchlings should be included in reports of the total population size.

When assessing rates of population increase with *C. porosus*, greater stability will result if the hatchling size class is deleted, and only non-hatchlings are considered (Fig. 5). This is because the number of hatchlings recruited into the population each year varies with the extent of nesting and embryonic mortality within nests. Within Northern Territory rivers, excluding hatchlings has the effect of increasing the annual rates of recovery by about 1.4% per year, while reducing the standard error of that estimate by about 0.1% (Table 6; see below).

Table 2. A comparison of two estimates of *Crocodylus porosus* habitat availability in the Northern Territory of Australia. MS = mainstream; SC = secondary creeks. *** the 1000 km of upstream freshwater channel estimated by Messel et al. (1981) equates approximately to the escarpment channel of Webb et al. (1984).

| Category | Webb et al. (1984) | | Messel et al. (1981, 1986) |
|---------------------------------------|-----------------------|-----------------|-------------------------------|
| Coastline | 8272 | km | 3200 km |
| Coastal secondary creeks | 1238 | km | - |
| Tidal river major breeding (MS+SC) | 1992 | km | 2175.5 km |
| Tidal river minor breeding (MS+SC) | 4325 | km | 2482.1 km |
| Flood plain channel | 1291 | km | - |
| Escarpment channel | 534 | km | 1000* km |
| Freshwater swamp | 3773 | km ² | - |
| Tertiary creeks | 8223 | ck's | - |

Table 3. Regions of the Northern Territory (Fig. 1) ranked according to the amounts of breeding and non-breeding habitat for *Crocodylus porosus* within them. Rank 1 = lowest and 10 = highest.

| Area | Breeding | | | Non-breeding | |
|----------|----------|-----------|-------|--------------|-------|
| | Swamp | F/Channel | Tidal | Coast | Tidal |
| Victoria | 1 | 2 | 1.5 | 3 | 10 |
| Daly | 10 | 7 | 5 | 2 | 1 |
| Darwin | 7 | 10 | 6 | 6 | 7 |
| Melville | 5 | 3 | 3 | 5 | 9 |
| Cobourg | 9 | 8 | 9 | 8 | 6 |
| Arnhem | 8 | 9 | 10 | 4 | 5 |
| Gove | 4 | 6 | 7 | 10 | 3 |
| Groote | 6 | 4 | 4 | 9 | 2 |
| Roper | 3 | 7 | 8 | 1 | 4 |
| Pellew | 2 | 1.5 | 1.5 | 7 | 8 |

Table 4. Areas of the Northern Territory (Fig. 1) ranked according to the abundance of all breeding habitat (rank 1 = highest). When hunters were questioned about the densities of *Crocodylus porosus* that existed in the late 1940s, at the start of commercial hunting, they identified 15 high density (6-12/km), 10 medium density (1-5/km), and 17 low density areas (<1/km) (Webb et al. 1984).

| Area | Breeding | Non-breeding | Historical Densities | | |
|----------|----------|--------------|----------------------|--------|-----|
| | | | High | Medium | Low |
| Arnhem | 10 | 3 | 2 | 4 | 6 |
| Cobourg | 9 | 9 | 3 | 2 | |
| Darwin | 8 | 6 | 5 | | |
| Daly | 7 | 1 | 2 | | |
| Roper | 6 | 2 | | 1 | 2 |
| Gove | 5 | 6 | 1 | 1 | 2 |
| Groote | 4 | 4 | 2 | 1 | 2 |
| Melville | 3 | 9 | | 1 | |
| Pellew | 2 | 9 | | | 3 |
| Victoria | 1 | 6 | | | 2 |

Table 5. The relationship between age and the probability of being represented in the river the following year for *Crocodylus porosus* in the Blyth-Cadell River system between 1974 and 1984 (data from Messel et al. [1981, 1984] and CCNT as analyzed by Webb et al. [1984]).

| Interval (years) | Mean | Maximum | Minimum |
|---------------------|------|---------|---------|
| 0.3-1.3 | 0.81 | 1.31 | 0.56 |
| 1.3-2.3 | 0.69 | 1.03 | 0.30 |
| 2.3-3.3 | 0.79 | 1.03 | 0.60 |
| 3.3-4.3 | 0.56 | 0.79 | 0.36 |
| 4.3-5.3 | 0.56 | 0.80 | 0.27 |

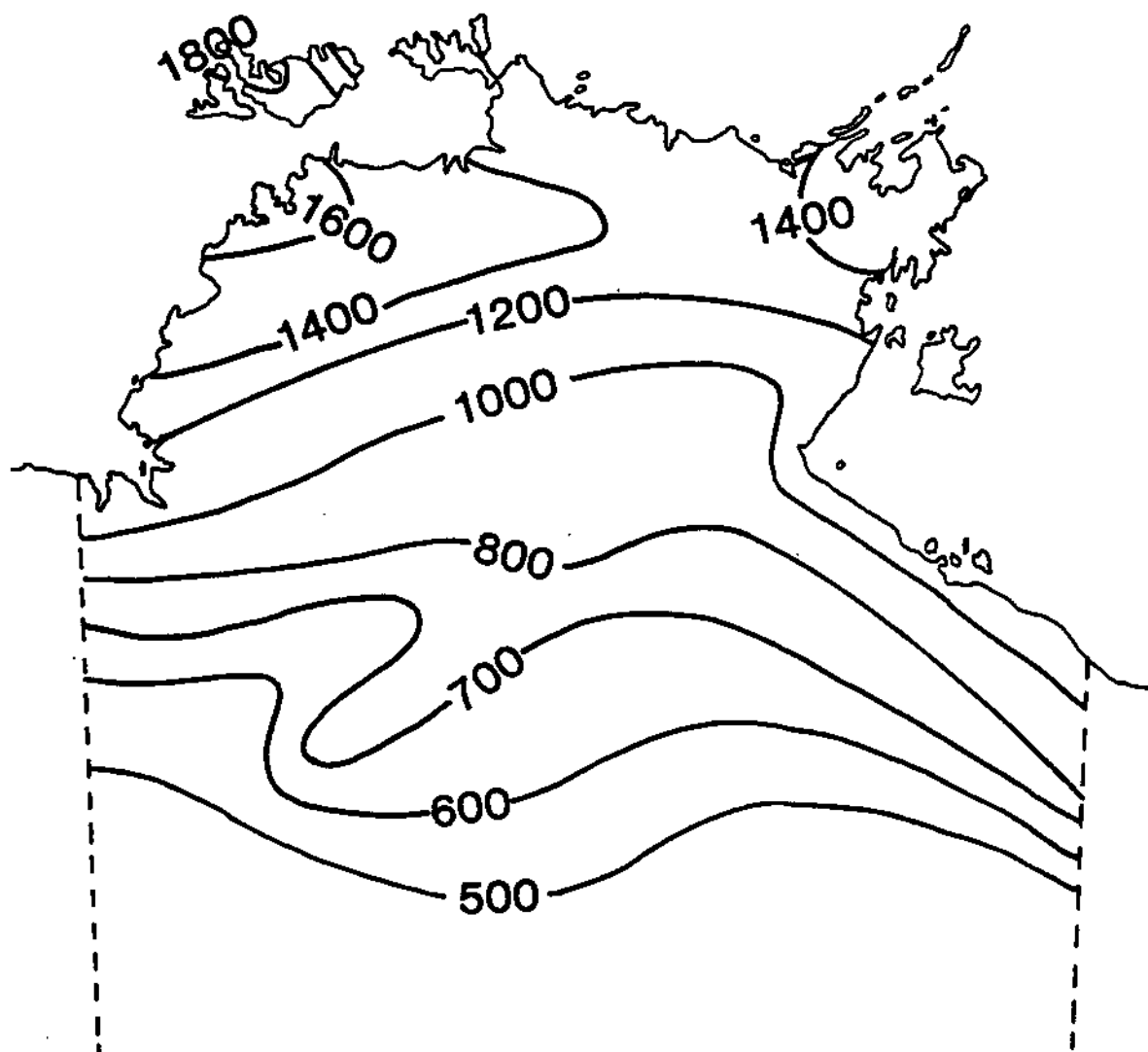


Figure 3. Mean annual rainfall (mm) in the Northern Territory (1873-1984).

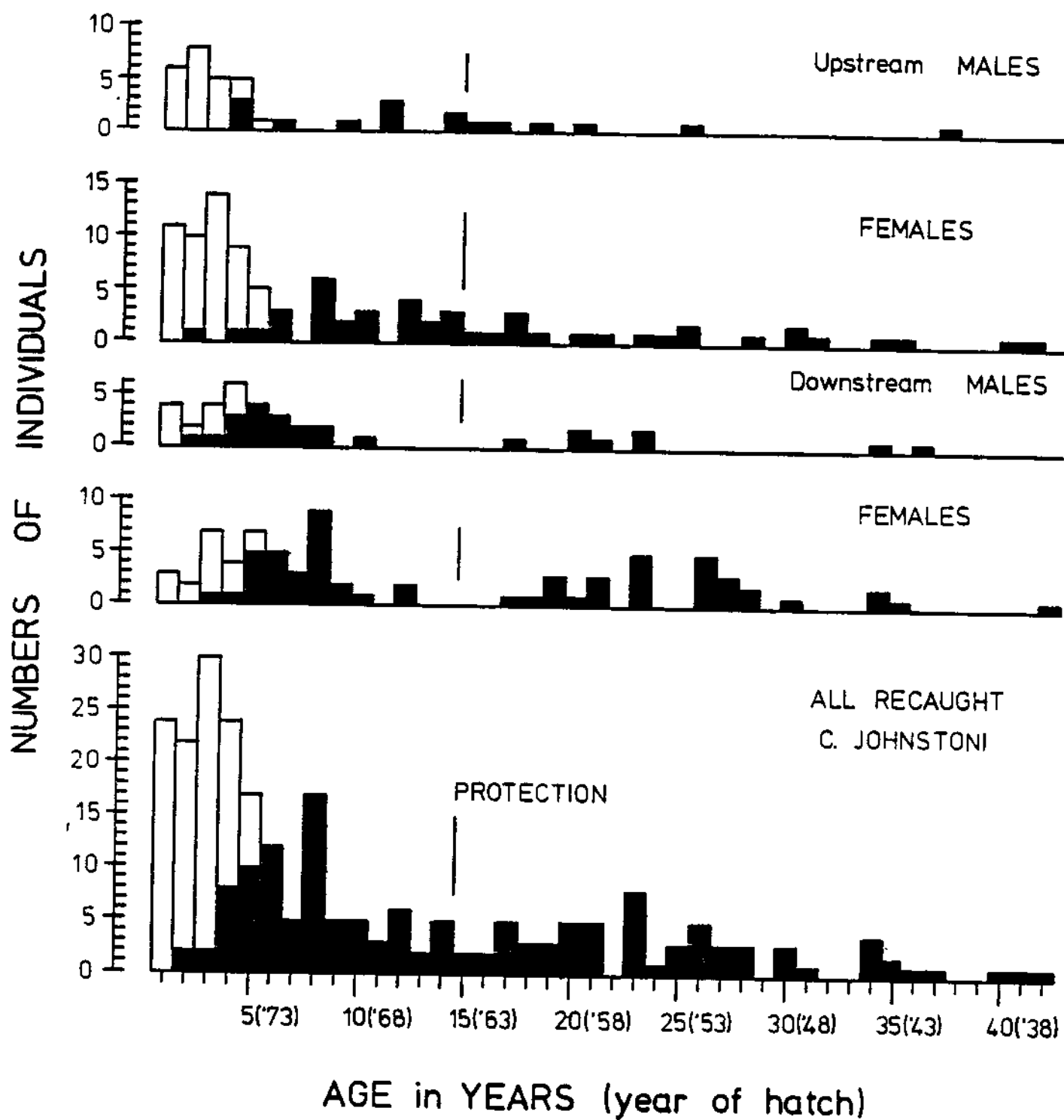


Figure 4. The age structure of a population of *Crocodylus johnstoni* within the Northern Territory (after Webb et al. 1983a).

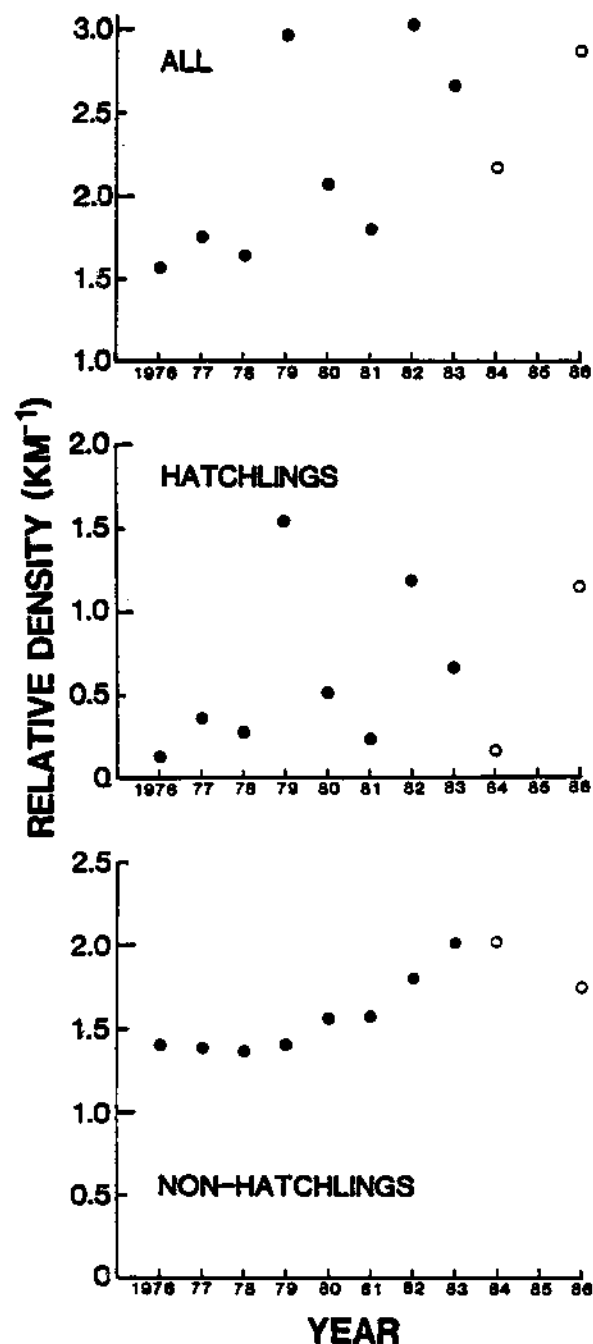


Figure 5. Relative densities of *Crocodylus porosus* in the Liverpool-Tomkinson River system. Closed circles indicate data from Messel et al. (1981) and open circles data from CCNT surveys.

RATES OF *C. POROSUS* RECOVERY

When the Northern Territory introduced protective legislation for *C. porosus* in 1971, the populations had been intensively hunted since 1945-46, and the adult population was reduced to a wary remnant. Within the first 2-5 years after protection, numbers increased rapidly in breeding areas (because recruits were not being harvested), although the average size of individuals was small. In some remote breeding areas this initial increase occurred prior to protection (Fig. 6).

Spotlight surveys carried out by the University of Sydney, the Conservation Commission of the Northern Territory (CCNT) and other organizations were initiated after this initial increase, and thus the analyses in Table 6 refer to rates of recovery from the mid-1970's to the mid-1980's - they underestimate the recovery of numbers that occurred between protection and the mid-1970's (Fig. 6).

These rates of recovery are based on spotlight counts alone and are not corrected for the changing size structure of the *C. porosus* population (see below). All regions from which there are survey data, indicate a positive rate of population increase among non-hatchlings - even low density areas such as Pellew (see Fig. 2). When all crocodiles were considered, the Roper region was the only one which did not have a similar positive rate of increase. It showed a 2.1% annual decrease between 1979 and 1985 [two spotlight surveys only; an additional survey in 1986 was by helicopter, and hatchlings are not detected], which was attributable to the lack of hatchlings counted in 1985 in one side creek of the Towns River (28 in 1979; 0 in 1985).

The exponential rates of increase are generally higher in the "non-hatchlings" than in "all crocodiles", and the mean rates for all areas combined are 8.3% p.a. (all crocodiles) and 9.7% p.a. (non-hatchlings). This is unequivocal evidence of an expanding population.

THE IMPACT OF HARVESTING *C. POROSUS* EGGS

During the 1983-84 season a preliminary one-day harvest of *C. porosus* eggs (994 eggs) was undertaken in the Adelaide River. However during the 1984-85 and 1985-86 *C. porosus* nesting seasons, experimental harvests (3517 and 3470 eggs respectively) were undertaken within parts of three river systems close to Darwin (Finniss, Reynolds, Adelaide; Fig. 2). Eggs from all nests were individually numbered and incubated under controlled conditions, and the post-hatching growth and survivorship of all resulting hatchlings (individually numbered by mutilating a known sequence of tail scutes), is now being monitored within the crocodile farms. The post-hatching performance of these individuals can be correlated with details of individual eggs, nests, habitats and incubation conditions.

All dead eggs were opened and the embryos were used to determine whether death had occurred before or after collection. As a consequence, the mortality within each area up until collection could be quantified (Table 7; data from the 1985-86 nesting season are not yet fully analyzed).

Harvesting eggs at an earlier stage of embryonic development was partly responsible for the reduced mortalities compared to wild incubation, but substantial losses in the field still occurred. These were due to flooding, overheating and what appeared to be asphyxia within sodden, muddy nests.

The impact of reducing hatchling recruitment by harvesting eggs could be expected to be detected in the 2-6' size class the following year. Spotlight surveys within the accessible parts of all areas harvested indicated no major decline in numbers, which is consistent with the view that harvests of eggs will result in a minimal impact on the size of wild populations (Webb et al. 1984, 1987). This approach to harvesting a wild population is atypical, as the general aim is usually to reduce densities to extract a sustainable yield

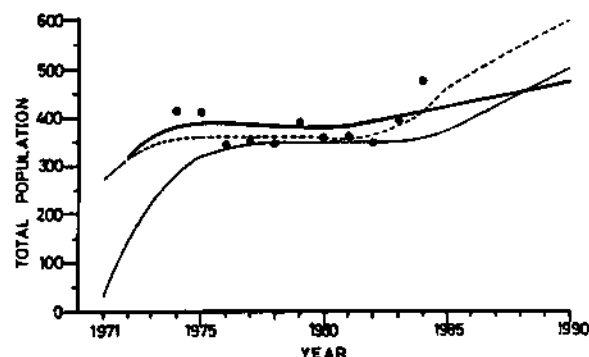


Figure 6. Total population estimates of *Crocodylus porosus* (excluding hatchlings) within the Blyth-Cadell River system as determined from corrected spotlight counts (dots). The dashed line represents the computer simulation of population predicted backwards to 1971 and forwards to 1990. The heavy line applies a density-dependent mortality among juveniles. The thin line does not apply density-dependent mortality, but assumes harvesting had continued up until protection, and that no juveniles were in the population at that time.

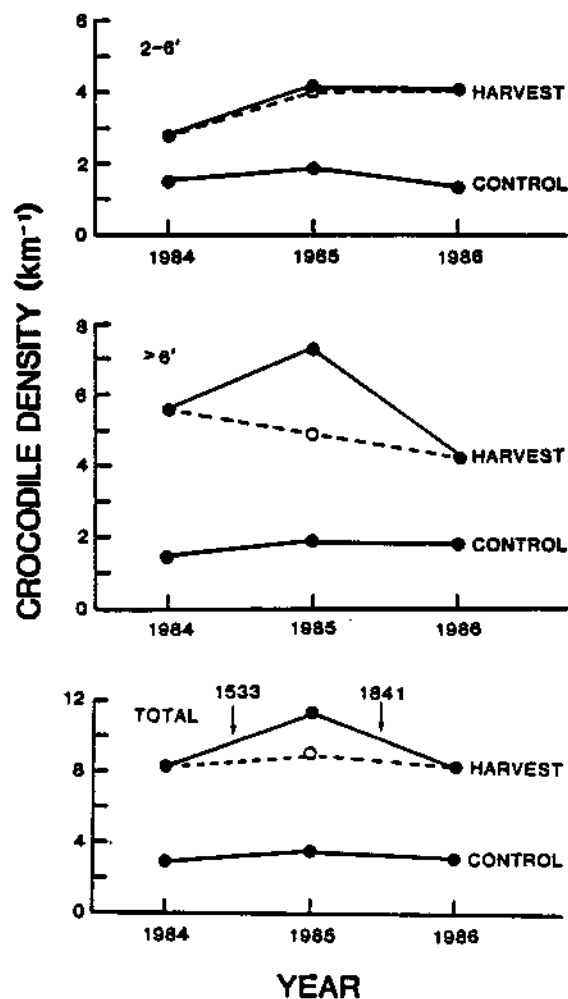


Figure 7. Relative densities of *Crocodylus porosus* in flood plain channels (Finniss-Reynolds River system) in which eggs were harvested and not harvested (1984-86). Numbers refer to the number of eggs harvested during a particular nesting season. Open circles indicate densities with one channel excluded (see text).

Table 6. Exponential annual rates of increase of *Crocodylus porosus* in major river systems within the Northern Territory between the mid-1970s and mid-1980s. Analyses are based on spotlight counts and/or helicopter counts standardized to spotlight counts. Original data from Messel et al. (1981,1986), Webb et al. (1984), and additional unpublished survey results from CCNT and ANPWS (Bayliss 1986). Rates are calculated for all crocodiles (T) and with hatchlings excluded (NH); R^2 is explained variance; *** only two surveys, regression analysis impossible.

| Area/River | Years | (N) | All Crocodiles | | | Non-Hatchlings | | |
|-----------------|---------|------|----------------|-------|------|----------------|-------|------|
| | | | r | R^2 | p | r | R^2 | p |
| DALY | | | | | | | | |
| Daly | 1978-86 | (4) | +0.104 | 0.91 | 0.10 | +0.103 | 0.95 | 0.05 |
| | MEAN | | +0.104 | | | +0.103 | | |
| DARWIN | | | | | | | | |
| Finnis | 1984-86 | (3) | +0.40 | 0.01 | NS | +0.038 | 0.01 | NS |
| Reynolds | 1984-86 | (3) | +0.130 | 0.03 | NS | +0.140 | 0.03 | NS |
| Adelaide | 1977-86 | (7) | +0.055 | 0.84 | 0.01 | +0.035 | 0.74 | NS |
| Mary | 1984-86 | (3) | +0.276 | 0.70 | NS | +0.276 | 0.70 | NS |
| | MEAN | | +0.125 | | | +0.122 | | |
| MELVILLE | | | | | | | | |
| Andranangoo | 1975-84 | (5) | +0.072 | 0.96 | 0.10 | +0.089 | 0.94 | 0.10 |
| Johnston | 1972-84 | (4) | +0.113 | 0.56 | NS | +0.110 | 0.55 | NS |
| Bath | 1972-84 | (4) | +0.134 | 0.74 | NS | +0.134 | 0.74 | NS |
| Dongau | 1972-84 | (6) | +0.016 | 0.03 | NS | +0.039 | 0.10 | NS |
| Tinganoo | 1972-84 | (5) | +0.181 | 0.73 | NS | +0.181 | 0.73 | NS |
| | MEAN | | +0.103 | | | +0.111 | | |
| COBOURG | | | | | | | | |
| Wildman | 1978-84 | (3) | +0.098 | 0.93 | NS | +0.153 | 0.74 | ns |
| W. Alligator | 1977-84 | (4) | +0.051 | 0.99 | 0.05 | +0.056 | 0.79 | NS |
| S. Alligator | 1977-84 | (10) | +0.225 | 0.27 | NS | +0.213 | 0.24 | NS |
| E. Alligator | 1977-85 | (8) | +0.072 | 0.64 | 0.01 | +0.058 | 0.64 | 0.01 |
| Murganella | 1977-84 | (4) | +0.096 | 0.57 | NS | +0.114 | 0.91 | NS |
| ARNHEM | | | | | | | | |
| King | 1975-79 | (4) | +0.240 | 0.74 | NS | +0.278 | 0.87 | NS |
| All-Night | 1975-79 | (3) | +0.271 | 0.39 | NS | +0.271 | 0.39 | NS |
| Goomadeer | 1975-84 | (8) | +0.016 | 0.06 | NS | +0.002 | 0.00 | NS |
| Majarie | 1975-84 | (7) | +0.040 | 0.18 | NS | +0.035 | 0.14 | NS |
| Wurugooj | 1975-84 | (7) | +0.139 | 0.38 | NS | +0.135 | 0.37 | NS |
| Liverpool- | | | | | | | | |
| Tomkinson | 1976-86 | (10) | +0.054 | 0.45 | 0.05 | +0.039 | 0.71 | 0.01 |
| Nungbulgarri | 1975-84 | (8) | +0.089 | 0.48 | NS | +0.071 | 0.36 | NS |
| Blyth-Cadell | 1974-86 | (13) | +0.002 | 0.00 | NS | -0.004 | 0.00 | NS |
| Crab | 1981-83 | (3) | +0.001 | 0.00 | NS | +0.001 | 0.00 | NS |
| Ngandadauda | 1975-83 | (3) | +0.029 | 0.92 | NS | +0.05 | 0.99 | 0.10 |
| Glyde | 1975-84 | (4) | +0.143 | 0.78 | NS | +0.153 | 0.98 | 0.05 |
| | MEAN | | +0.093 | | | +0.094 | | |

GOVE

| | | | | | | | | |
|----------------|---------|-----|--------|------|----|--------|------|----|
| Darwarunga | 1975-84 | (3) | +0.129 | 0.89 | NS | +0.126 | 0.90 | NS |
| Habgood | 1975-84 | (3) | +0.081 | 0.89 | NS | +0.095 | 0.80 | NS |
| Habgood Ck | 1975-84 | (3) | +0.001 | 0.00 | NS | +0.001 | 0.00 | NS |
| Baralminar | 1975-84 | (3) | +0.096 | 0.89 | NS | +0.096 | 0.89 | NS |
| Gobolpa | 1975-84 | (3) | +0.075 | 0.83 | NS | +0.091 | 0.93 | NS |
| Goromuru | 1975-84 | (3) | +0.006 | 0.06 | NS | +0.050 | 0.82 | NS |
| Cato | 1975-84 | (3) | +0.015 | 0.25 | NS | +0.101 | 0.92 | NS |
| Peter John | 1975-84 | (3) | -0.018 | 0.03 | NS | -0.004 | 0.01 | NS |
| Burungbirinung | 1975-84 | (3) | +0.096 | 0.52 | NS | +0.222 | 0.65 | NS |
| MEAN | | | +0.053 | | | +0.086 | | |

ROPER*

| | | | | | | | | |
|--------------|---------|-----|--------|---|---|--------|------|----|
| Limmen Bight | 1979-86 | (3) | +0.061 | - | - | +0.077 | 0.94 | NS |
| Towns | 1979-86 | (3) | -0.110 | - | - | +0.006 | - | - |
| Roper | 1979-86 | (3) | -0.015 | - | - | +0.017 | - | - |
| MEAN | | | +0.021 | | | +0.033 | | |

PELLEW

| | | | | | | | | |
|------------------|---------|-----|--------|---|---|--------|------|------|
| McArthur | 1979-86 | (3) | +0.055 | - | - | +0.054 | 0.99 | 0.10 |
| Wearyan-Foelsche | 1979-86 | (3) | +0.035 | - | - | +0.021 | 0.37 | NS |
| MEAN | | | +0.045 | | | +0.038 | | |

MEAN OF ALL AREAS

(SE) ± 0.013 ± 0.012

%pa

+8.3

+9.7

(N)

40

40

Table 7. Results of the experimental *Crocodylus porosus* egg harvest in 1984-85 compared to results for wild nests in two of the same areas in the 1980-81 season.

| Area: | Melacca | Melacca | Adelaide | Finniss-Reynolds | Finniss-Reynolds |
|----------------------|---------|---------|----------|------------------|------------------|
| Season | 1980-81 | 1984-85 | 1984-85 | 1980-81 | 1984-85 |
| Wild or harvest | wild | harvest | harvest | wild | harvest |
| Nests examined | 18 | 19 | 22 | 33 | 26 |
| Eggs examined | 917 | 959 | 1025 | 1795 | 1533 |
| Eggs hatched (%) | 35.6 | 80.3 | 59.2 | 29.2 | 45.7 |
| Eggs infertile (%) | 9.4 | 3.6 | 7.9 | 5.0 | 5.4 |
| Eggs damaged (%) | 0.6 | 0.8 | 0.4 | 2.4 | 2.3 |
| Eggs failed | | | | | |
| 1. in field (%) | 54.4 | 9.6 | 17.9 | 62.8 | 26.0 |
| 2. in laboratory (%) | - | 5.6 | 14.6 | - | 20.5 |

(Caughley 1977). Populations at equilibrium are often reduced by 30-50% (depending on the harvest model used) to achieve maximum sustained-yield.

In the Finnis-Reynolds area (Fig. 7), some channels were harvested and others were not. Analysis of variance of density trends between harvested and unharvested areas (Table 8) showed no significant effect of harvest (the time by experiment interaction was not significant). There was a significant three-fold difference in the densities between the harvested and unharvested areas (Fig. 7), which indicates that harvests were concentrated in the flood plain channels with the highest densities of crocodiles. An increase in the number of >6' animals in 1985 (Fig. 7) was largely due to increased numbers of >6' animals in one harvested channel, but this effect was trivial (time by size class interaction was not significant; Table 8), and unrelated to the harvest of eggs.

In the Adelaide River, no local control was available and so the Liverpool-Tomkinson data were used as a control of sorts. This population is within a tidal breeding system (as is the Adelaide) and had:

1. Similar non-hatchling densities between 1977 and 1979, well before the egg harvests, (Fig. 8); and,
2. A positive rate of increase after 1977-79 (Fig. 8), as did the Adelaide River.

The Blyth-Cadell system, which has been surveyed more regularly, was rejected as a control because its rate of increase was close to zero - lower than that of the harvested population.

Because of the more extensive survey data, analysis of covariance was used to test for differences in density trends over time (Table 9). No significant difference in the average exponential rates of increase (all crocodiles) between the two populations could be demonstrated, regardless of size class (Table 10), indicating no major effect of the harvest (as is obvious from Fig. 9).

Taken together, the survey results from the Adelaide and Finnis-Reynolds areas indicate that some 7,981 eggs were collected from 162 wild nests within 140 km of Darwin, with no significant impact on the wild populations. More data are needed to quantify subtle or longer-term effects, and the study is continuing, but results to date are consistent with predictions of a minor impact.

FLOOD-PRONENESS OF *C. POROSUS* NESTS

A detailed analysis of flood mortality among eggs collected to date is currently being undertaken. Melacca Swamp (our main monitoring area for *C. porosus* nesting), is the least "flood-prone" of the areas currently under study, and mortality due to flooding was modelled over the period 1960-61 to 1980-81 (Webb et al. 1983c). The results indicate flood losses ranging from 0% to 50% per annum, depending on the pattern of annual rainfall (mean = 26%); this indicates a total mortality of between about 20% and 70% of eggs per year (mean = 46%). The degree to which individual nests are prone to mortality due to flooding is largely unpredictable, due to the equally unpredictable timing and extent of wet season rains.

Our random egg harvest (see above) did not appear to have any major impact on the populations, and for economic and safety reasons, the main criteria for an efficient harvest in the future will be the accessibility of nests to collectors, and the number of nests available at the time of collection. By leaving a random sample of nests (those that are inaccessible for a variety of reasons), and by concentrating the harvest at the peak of nesting, the impact should be less than that currently experienced. Attempts to incorporate a predicted probability of embryo mortality (due to flooding, overheating, predation etc.) into the current harvest strategy, may well prove to be costly and cosmetic.

Table 8. Analysis of variance of small (2-6') and large >6') *Crocodylus porosus* density trends between flood plain channels that are harvested for eggs (treatment) and those that are unharvested (control) in the Finnis-Reynolds Rivers system, 1984-86. Relative densities are transformed to natural logarithms. '*' this interaction tests the egg-harvest response. NS = not significant; E = experiment (treatment and control); T = time in years. Flood plain channels are treated as replicates (N=4).

| Source | SS | d.f. | MS | F | Significance |
|-----------------------|-------|------|------|-------|--------------|
| Harvest-unharvest (E) | 5.49 | 1 | 5.49 | 16.64 | $p < 0.001$ |
| Time (T) | 0.58 | 2 | 0.29 | 0.88 | NS |
| Size-class (S) | 0.45 | 1 | 0.45 | 1.36 | NS |
| E.T* | 0.02 | 2 | 0.01 | 0.03 | NS |
| T.S | 0.03 | 2 | 0.01 | 0.03 | NS |
| E.S | 0.17 | 1 | 0.17 | 0.51 | NS |
| E.T.S | 0.31 | 2 | 0.15 | 0.45 | NS |
| Residual | 11.75 | 36 | 0.33 | | |
| Total | 18.79 | 47 | | | |

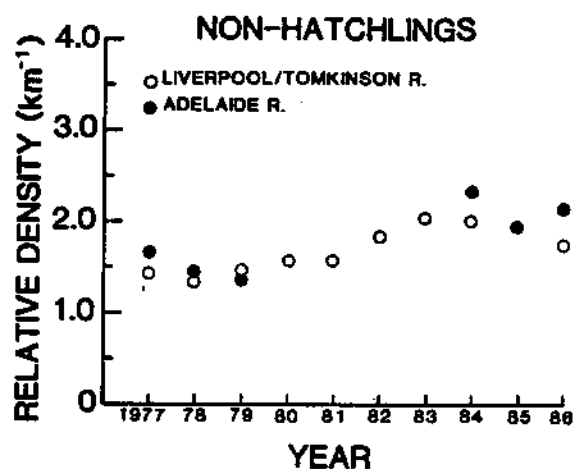


Figure 8. Relative densities of non-hatchling *Crocodylus porosus* in the Adelaide and Liverpool-Tomkinson Rivers, 1976-1986. Closed circles indicate data from Messel et al. (1981, 1986) and open circles indicate data from Webb et al. (1984, unpubl. data).

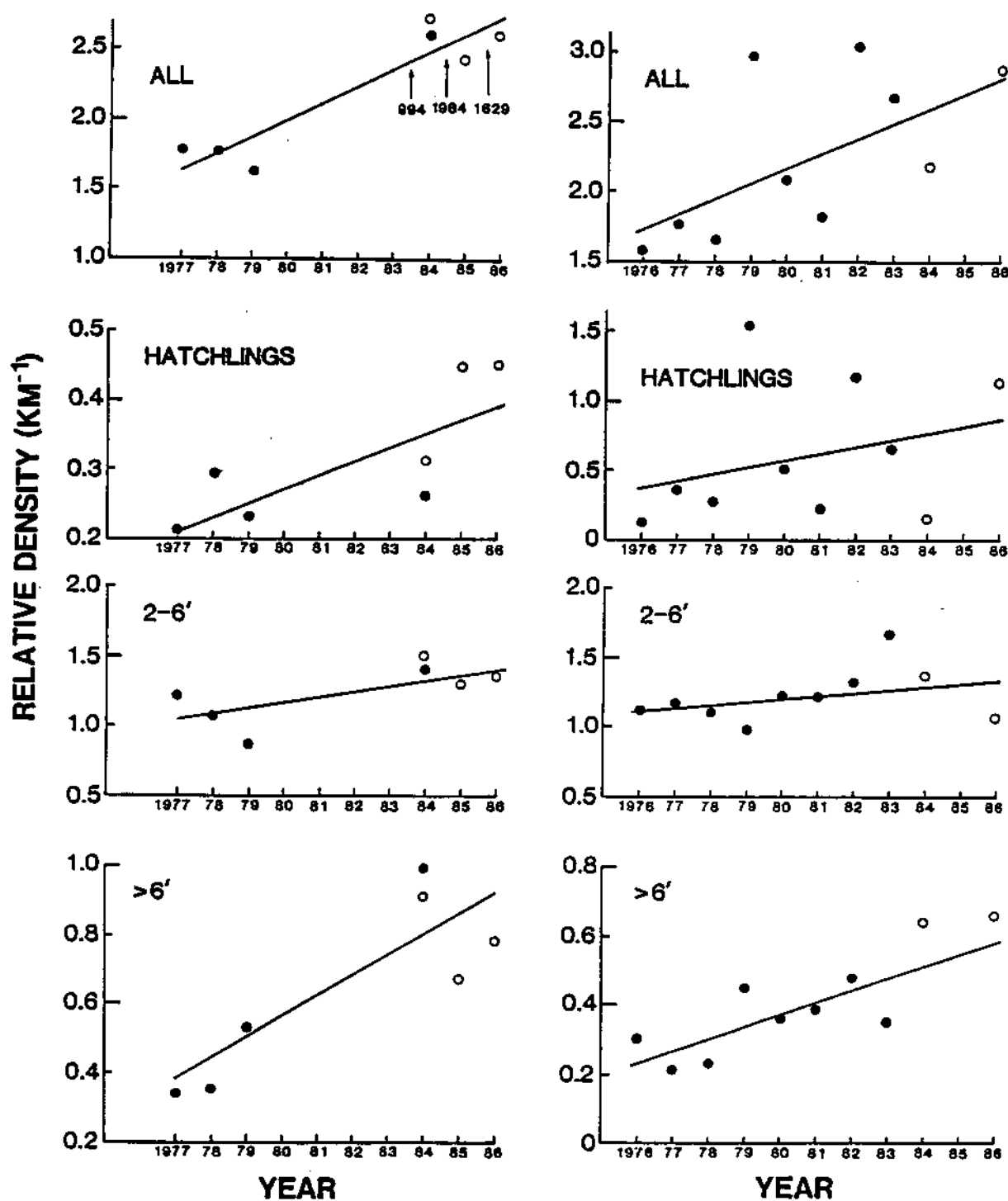


Figure 9. Relative densities of *Crocodylus porosus* in the Adelaide (harvested) and Liverpool-Tomkinson River (unharvested) systems. Numbers refer to the numbers of eggs harvested in a particular nesting season. Closed circles indicate surveys by Messel et al. (1979b, 1981, 1986), and open circles are surveys by the CCNT. Lines indicate the average exponential rates of increase derived by linear regression analysis.

Table 9. A summary of an analysis of covariance between *Crocodylus porosus* density trends in the Adelaide River (eggs are harvested) and the Liverpool-Tomkinson Rivers (eggs are unharvested), 1976-1986. Densities are transformed to natural logarithms. 'Slopes' test significant differences between the average annual exponential rates of increase (r). NS = not significant.

| Source | d.f. | F-ratio | Significance |
|------------|------|---------|--------------|
| Slopes | 1.11 | 0.01 | NS |
| Intercepts | 1/12 | 0.90 | NS |

Table 10. Exponential annual rates of increase of *Crocodylus porosus* populations in the Adelaide and Liverpool-Tomkinson Rivers, with standard errors (SE) of the slope and significance of the regression; ** = $p < 0.05$, *** = $p < 0.01$, NS = not significant.

| River | Size Class | r (p.a.) | SE | Significance |
|---------------------|---------------|------------|-------|--------------|
| Adelaide | All | 0.055 | 0.011 | ** |
| | Hatchling | 0.065 | 0.021 | * |
| | 2-6' | 0.034 | 0.017 | $p < 0.10$ |
| | >6' | 0.099 | 0.024 | * |
| | Non-hatchling | 0.054 | 0.014 | * |
| Liverpool-Tomkinson | All | 0.054 | 0.021 | * |
| | Hatchling | 0.108 | 0.094 | NS |
| | 2-6' | 0.020 | 0.015 | NS |
| | >6' | 0.090 | 0.020 | * |
| | Non-hatchling | 0.039 | 0.009 | ** |

ESTIMATING CROCODILE TOTAL LENGTHS

Estimating the total lengths of crocodiles sighted during spotlight and helicopter counts expands the information contained in survey results. However, many factors affect the ability of an observer to estimate the size of a crocodile accurately (Magnusson 1983), and the precision of such estimates has rarely been quantified. Choquenot and Webb (1987) used a calibrated camera to examine the accuracy of two experienced observers (Fig. 10), and found that one (Observer A) was erratic over all size classes when compared to the other (Observer B).

Observers also vary in the consistency with which they estimate the lengths of the same crocodiles, in the same areas, as found by Messel et al. (1981). For example, when we examined data from re-surveys of the same flood plain channel with the same observer, on six separate occasions, during the same night, a significant relationship was found between the numbers of 2-6' and >6' crocodiles sighted (Fig. 11). These data suggest that, animals in the 2-6' category on one survey were placed within the >6' category in another, because of random error in estimating lengths.

The same type of variation occurs in data collected by different survey teams. Approximately the same number of crocodiles are sighted at the same time (Table 11), but the size estimates and proportions of "eyes only" can vary significantly (Table 12). In the Adelaide River (1984), the CCNT survey teams were apparently more cautious in allocating lengths to crocodiles sighted - they were more likely to place an animal within the "eyes only" category (Table 12).

There appears to be no simple solution to the problem of standardizing observer length estimates, because in addition to variable precision and accuracy, there may be drift with observers who are not regularly sighting and catching crocodiles. A calibrated camera technique (Choquenot and Webb 1987) could overcome some of these problems, and merits further investigation.

In the interim, caution needs to be exercised in the extent to which length estimates are incorporated into bold conclusions about short-term changes in the size and age structure of populations. The size estimating procedure is inherently inaccurate, and long-term data are needed to separate variability due to observers from that due to real changes in the structure of the population.

CORRECTION FACTORS FOR SPOTLIGHT COUNTS

Spotlight counts provide precise relative density indices which can be used to monitor population rates of increase, but they are inherently inaccurate (Bayliss 1987). Animals are usually missed on surveys and deviations from absolute density is termed visibility bias. Correction factors which can be applied to relative density indices are needed to:

1. Standardize relative density indices for any size-related bias in sightability, which could affect the stability of the index over time (if the average size or level of wariness is increasing or decreasing) or in different areas (where the size or wariness of individuals varies);
2. Adjust the relative density indices in habitats where there are different probabilities of detection, to afford comparison;
3. Correct relative density indices to absolute densities for estimating the total population size.

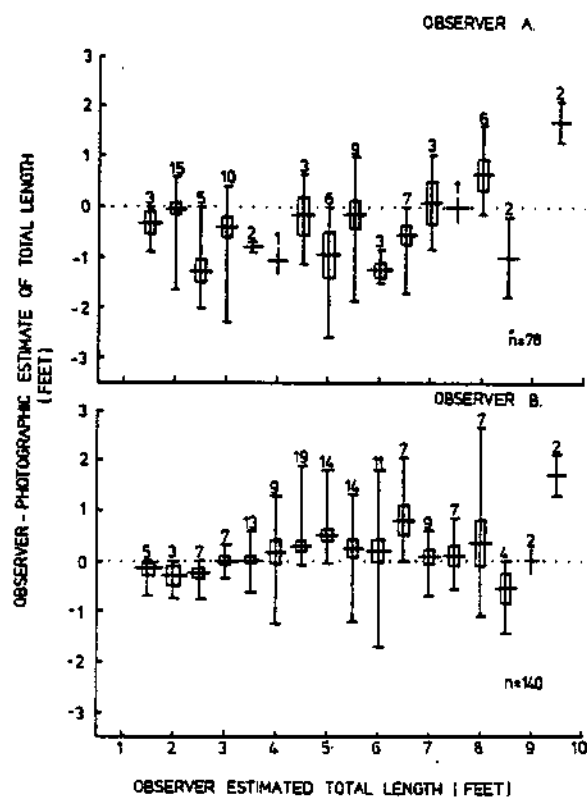


Figure 10. A comparison of spotter estimated sizes (to the nearest half-foot) and those estimated from a photographic method (Choquenot and Webb 1987) for *Crocodylus porosus* sighted during spotlight surveys in the Adelaide River. All photographs were analyzed by the same person. Horizontal lines are the means and ranges; boxes are one standard deviation (SD) on either side of the mean; numbers are the sample sizes for each half-foot category. Values above the broken line indicate an observer is overestimating the size of crocodiles sighted.

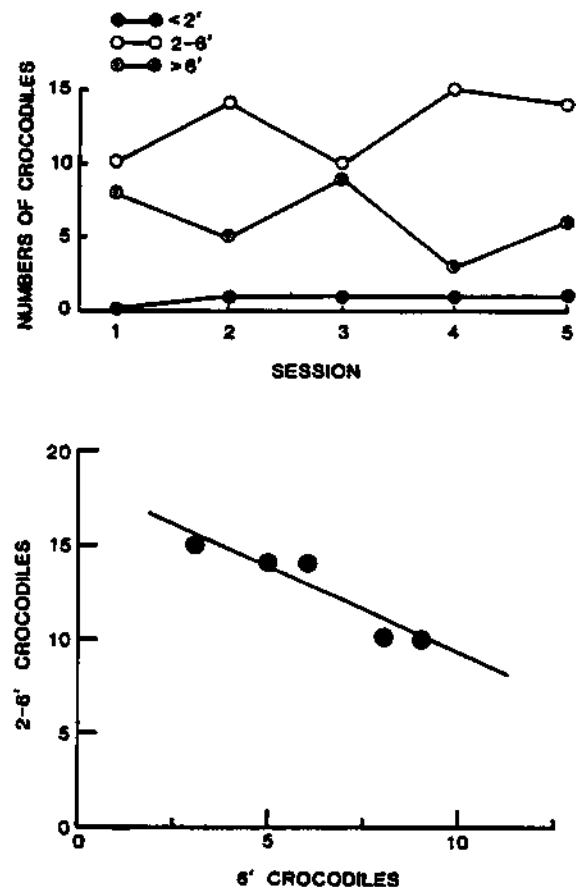


Figure 11. Numbers of different sized *Crocodylus porosus* sighted over five sessions in a flood plain channel of the Finniss River (upper); and the relationship between the number of 1-6' (Y) and >6' (X) crocodiles in the same channel (lower), $Y = 18.5 - 0.95X$ ($r^2 = 0.88$, $n = 5$, $p < 0.025$).

Table 11. Relative densities of three river systems surveyed independently by the University of Sydney (US; Messel et al. 1986), the Conservation Commission of the Northern Territory (CCNT), and Australian National Parks and Wildlife Service (ANPWS). Also presented is the linear regression equation for these data. "*" = hatchlings excluded.

| Relative Density (km^{-1}) | | | |
|--|-------|------|------------------|
| CCNT-ANPWS | US | Year | River |
| 2.718 | 2.606 | 1984 | Adelaide |
| 0.207 | 0.206 | 1985 | McArthur |
| 0.116 | 0.145 | 1985 | Wearyan-Foelsche |
| 3.229 | 3.114 | 1984 | East Alligator* |
| Calibration Equation | | | |
| $\text{US} = 0.021 + 0.955 (\text{CCNT-ANPWS})$ $(R^2 = 1.00, n=4, p<0.001)$ | | | |

Table 12. The size distribution of *Crocodylus porosus* sighted in two independent spotlight surveys of the Adelaide River, at the same time of year, in 1984.

| | Messel et al. (1986) | | CCNT (unpublished) | |
|---------------------|----------------------|-----|--------------------|-----|
| | % | No. | % | No. |
| Hatchlings | 9.6 | 60 | 12.7 | 80 |
| 2-3' | 5.8 | 36 | 8.9 | 56 |
| 3-4' | 16.8 | 105 | 11.1 | 70 |
| 4-5' | 12.6 | 79 | 7.6 | 48 |
| 5-6' | 10.2 | 64 | 9.4 | 59 |
| 6-7' | 12.5 | 78 | 7.0 | 44 |
| >7' | 19.2 | 120 | 15.2 | 96 |
| "Eyes only" | 11.7 | 73 | 25.9 | 163 |
| <i>C. johnstoni</i> | 1.8 | 11 | 2.2 | 14 |
| Totals | | 626 | | 630 |

1. How Precise are Spotlight Counts?

Replicated surveys of *C. porosus* in tidal rivers and flood plain channels show high precision (Table 13), even with a small number of samples. This precision was even maintained during sessions in which tags were harpooned into the crocodiles in flood plain channels (Fig. 12).

2. Relating Spotlight Counts to Absolute Numbers in Tidal Rivers and Flood Plain Channels

Bayliss et al. (1986) estimated the total population of *C. porosus* within three sections of the Adelaide River using a mark-recapture technique, and obtained a precise estimate of the total population size. They then quantified mean sighting fractions seen in spotlight surveys in each of the three areas (Table 14).

More recently, the same mark-recapture technique was used to estimate the total population of *C. johnstoni* and *C. porosus* in two isolated sections of flood plain channel which were bordered by floating mats of vegetation; sighting fractions were derived in the same way (Table 14). Additional correction factors for *C. johnstoni* in isolated flood plain billabongs devoid of floating vegetation were derived from data in Webb et al. (1983b).

3. Relating Spotlight Counts to Helicopter Counts

Spotlight surveys have other major limitations besides inherent visibility bias. They are time-consuming, expensive, often dangerous, and more importantly, are restricted to habitats that are accessible by boat. There are large areas of crocodile habitat in the Northern Territory that have not been surveyed due to poor or impossible boat access. For *C. porosus*, helicopter surveys are much cheaper and less time-consuming than boat surveys, yet they provide an index of density that relates to that obtained by spotlighting (Bayliss et al. 1986). Helicopter counts are similar to spotlight counts in tidal rivers with large exposed mud-banks, but in tidal sidecreeks they are almost double that of spotlight counts, and hence require a different calibration equation (Table 15). Thus, helicopter surveys can be used to derive different calibration equations for spotlight counts in different habitats. For example, spotlight counts in tidal side creeks record only a small proportion of the total population in such creeks (Bayliss et al. 1986; 35%) due to stream sinuosity (Fig. 13), and these problems are largely overcome by aerial survey.

Helicopter survey techniques are also being developed for *C. johnstoni*, (which is more difficult to see from the air), and the results are also summarized in Table 15. The *C. johnstoni* calibration equation is preliminary and will be refined with additional data from surveys in 1986.

The validity of the equations relating helicopter counts to spotlight counts derived in the Adelaide River were tested in a low density area in 1986. Sections of the McArthur River were surveyed by helicopter in September during high and low bank exposure, and the calibrated helicopter counts were compared to spotlight counts in the same area (Table 16). Even though the relative density was one-twelfth that in the Adelaide River, the calibration equations were applicable. Subsequently, three major river systems (remainder of the McArthur, Limmen Bight, Wearyan-Foelesche) and 25 coastal creeks in the southern Gulf of Carpentaria were surveyed over a two day period, at half the cost of spotlight surveys and taking one-sixth the time. (Surveys in less remote areas can be surveyed at one-quarter the cost of spotlight surveys.)

Table 13. The precision of *Crocodylus porosus* and *C. johnstoni* spotlight counts in different habitats. Data are from: 1 = Messel et al. (1981); 2 = Bayliss et al. (1986); 3 = CCNT (unpubl.). "*" indicates precision measured on sessions where tags were being harpooned into the crocodiles; DS = downstream, US = upstream.

| Area | Habitat | Mean N Sessions | | SE (in %) |
|-----------------------------|----------------------------|-----------------|-------|-----------|
| <i>Crocodylus porosus</i> | | | | |
| Blyth ¹ | Mainstream, tidal, DS | 55-66 | 28-27 | 1.1-3.7 |
| Blyth ¹ | Mainstream, tidal, US | 39-42 | 15 | 2.0-4.0 |
| Adelaide ² | Mainstream, tidal, DS | 88 | 2 | 0.6 |
| Adelaide ² | Mainstream, tidal, US | 32 | 2 | 3.1 |
| Adelaide ² | Sidecreeks, tidal, DS | 30 | 2 | 1.6 |
| Finniss ³ | Flood plain channel No. 1 | 47 | 5 | 3.1 |
| Finniss ³ | Flood plain channel No. 2* | 36 | 7 | 9.7 |
| <i>Crocodylus johnstoni</i> | | | | |
| Finniss ³ | Flood plain channel No. 2* | 74 | 7 | 7.1 |

Table 14. The mean probability (p) of sighting crocodiles on spotlight surveys in different habitats, with the correction factors (CF) needed to adjust relative densities to absolute densities. Data are from: 1 = Bayliss et al. (1986); 2 = Webb et al. (1983b); 3 = CCNT (unpubl. data).

| River | Habitat | Year | p | CF |
|-----------------------------|---|------|------|------|
| <i>Crocodylus porosus</i> | | | | |
| Adelaide ¹ | Tidal; downstream | 1984 | 0.66 | 1.51 |
| Adelaide ¹ | Tidal; upstream | 1984 | 0.59 | 1.69 |
| Adelaide ¹ | Mean mainstream | | | 1.60 |
| Adelaide ¹ | Tidal; side creeks | 1984 | 0.35 | 2.86 |
| Finniss ³ | Non-tidal; flood plain channel No. 1 | 1986 | 0.64 | 1.56 |
| Finniss ³ | Non-tidal; flood plain channel No. 2 | 1986 | 0.51 | 1.96 |
| Finniss | Mean non-tidal; flood plain channel | | | 1.76 |
| <i>Crocodylus johnstoni</i> | | | | |
| Finniss ³ | Non-tidal; flood plain channel No. 2 | 1986 | 0.44 | 2.27 |
| McKinlay ² | Non-tidal; billabongs; no floating vegetation | 1978 | 0.66 | 1.51 |

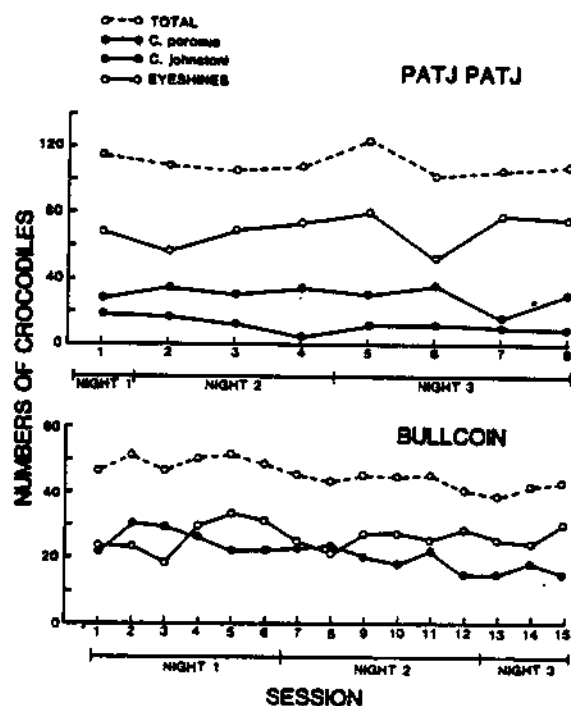


Figure 12. Numbers of crocodiles sighted in two flood plain channels in the Finnis River during a mark-recapture experiment (see text).

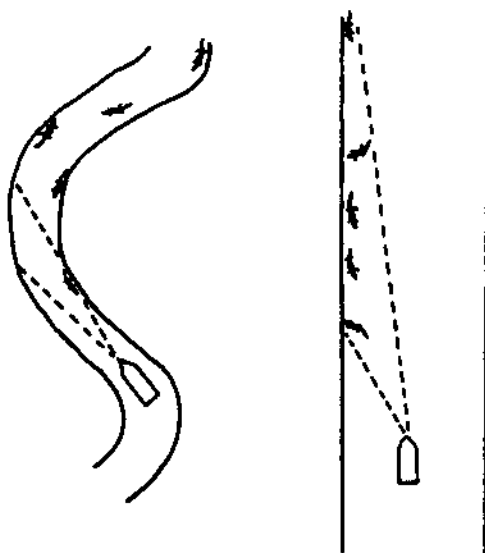


Figure 13. Schematic representation of spotlighting in a mainstream tidal river (left) and a tidal side creek (right). Crocodiles that are a considerable distance from the boat can be counted as eyeshines if they submerge before they have been reached. In side creeks, crocodiles usually submerge close to the survey boat before being detected.

Table 15. Summary of equations used to standardize helicopter counts to spotlight counts. Data are from Bayliss et al. (1986) and unpublished survey results from the CCNT. Equations were derived by linear regression analysis; S = spotlight counts, H = helicopter counts, Banks = number of banks surveyed by helicopter.

| Habitat | Banks | Tide | Equation | R ² | N | Significance |
|-----------------------------|-------|--------|--------------------|----------------|----|--------------|
| <i>Crocodylus porosus</i> | | | | | | |
| Tidal mainstream | 1 | Spring | $S = 2.07H$ | 0.98 | 7 | $p < 0.001$ |
| Tidal mainstream | 1 | Neap | $S = 3.18H$ | 0.96 | 8 | $p < 0.001$ |
| Tidal side creeks | 2 | Neap | $S = 0.55H$ | 0.99 | 4 | $p < 0.001$ |
| <i>Crocodylus johnstoni</i> | | | | | | |
| Non-tidal | 1 | | $S = 64.8 + 7.39H$ | 0.76 | 37 | $p < 0.001$ |

Table 16. Comparison between helicopter counts converted to spotlight counts and actual spotlight counts of *Crocodylus porosus* and *C. johnstoni* in a section of the McArthur River. Equations used to convert the helicopter counts to spotlight counts for high (spring) and low (neap) tide bank exposures were derived in the Adelaide River (see Table 15). Data refer to non-hatchlings only.

| Bank Exposure | Methods | <i>C. porosus</i> | <i>C. johnstoni</i> |
|---------------|------------|-------------------|---------------------|
| Low | Helicopter | 28 | 4 |
| High | Helicopter | 28 | 3 |
| High | Spotlight | 28 | 3 |

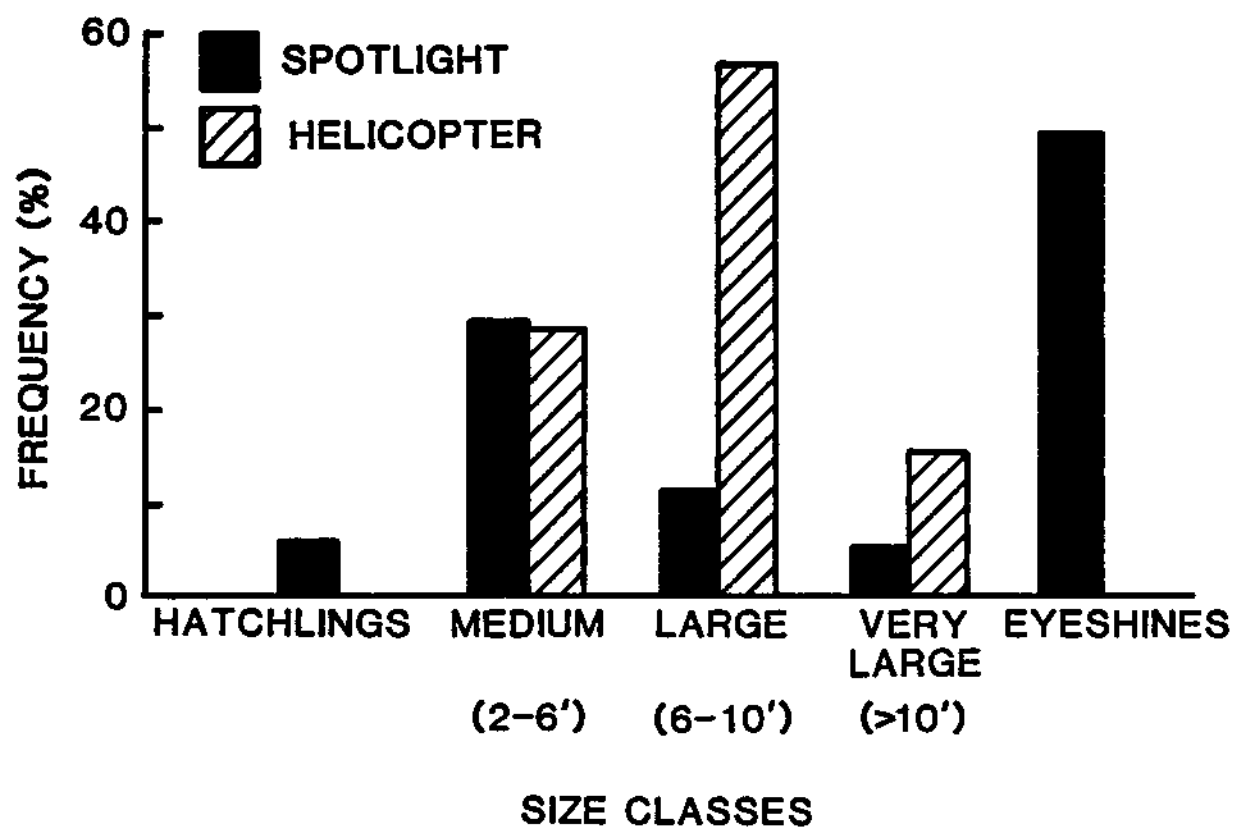


Figure 14. Proportions of hatchlings, 2-6', >6', and eyeshines sighted in spotlight and helicopter surveys in the McArthur River, a low density area.

The size classes of crocodiles seen in helicopter surveys in the McArthur River suggest that the "eyes only" fraction seen in spotlight surveys in this river should be apportioned to the greater than 6' category (Fig. 14), which are presumably more wary of spotlights.

Although there are advantages in spotlight surveys (e.g., a more accurate assessment of the age-size structure of the population, and the proportion of animals that are hatchlings) helicopter surveys are cost-effective and provide most of the information necessary to determine relative distribution and abundance patterns, and to assess long-term trends in the numbers of non-hatchlings. A further advantage is the ability to improve the precision of a population index rapidly by replication at a reasonable cost.

Future research will involve further refinement of the helicopter census technique for both *C. porosus* and *C. johnstoni*, and on calibrating *C. porosus* nest counts by helicopter to estimates of absolute crocodile numbers in habitats that are impossible or difficult to survey by spotlight or helicopter (e.g. densely vegetated freshwater swamps).

4. Relating Absolute Numbers in Flood Plain Channels and Tidal Rivers to Nest Numbers

During the 1984-85 and 1985-86 wet seasons, intensive surveys of *C. porosus* nests were carried out in parts of the Adelaide, Finniss and Reynolds Rivers. These same areas were surveyed by spotlight in 1984, 1985 and 1986, and in three areas the total population of *C. porosus* was estimated using the corrections in Table 14. Accordingly, a relationship was derived between numbers of nests and the total population size (Table 17).

The results indicate that the nesting female portion of the population varies from 4.3% to 13.9% of the total population, with a mean value of 5.7% (6.5% for non-hatchlings). This percentage in turn can be used to estimate the total population of *C. porosus* in breeding areas where nests can be counted. Population monitoring of *Alligator mississippiensis* in Louisiana, where nesting females represent 5% of the population, is based solely on correcting nest counts in this fashion (Joanen and McNease 1986).

Nest counts may also be a more accurate index of the adult crocodile population in areas where females are wary or where they reside outside of the accessible mainstreams. For example, Messel et al. (1979b) counted 3 crocodiles greater than 7' in length in spotlight counts within the Liverpool-Tomkinson River system in 1976, yet there were 38 nests in one season in the same area (Messel et al. 1981). As maturity is reached at 7-8' in females and >11' in males, there were at least some 40-50 crocodiles >7' in the system although only three were sighted (some were no doubt within the "eyes only" category).

5. Standardizing for Size in Spotlight Counts

Large *C. porosus* are more wary than smaller ones (Webb and Messel 1979), and have lower probabilities of being sighted in spotlight surveys (Bayliss et al. 1986). This trend was as apparent 13 years after protection (Bayliss et al. 1986), as it was 4 years after protection (Webb and Messel 1979), and thus it does not appear to be totally explicable on the basis of learned behavior among the older crocodiles which experienced hunting prior to protection (<1971). Increased size appears to be inherently associated with increased wariness in *C. porosus* (Table 18).

Within recovering populations, where the mean size of individuals is increasing with time, size-dependent wariness causes an increasingly pronounced negative bias in density indices. For example, if 105 crocodiles were sighted in a tidal river in 1975, and they were composed of 100 3-4' and 5 7-8' crocodiles, it would indicate a total population of 139 [Table 18; $(100 \times 1.30) + (5 \times 1.71)$]. If in 1984 the same number of individuals (105) was sighted, it may superficially appear that the rate of recovery had been zero. Even if

Table 17. The relationship between numbers of *Crocodylus porosus* nests made during the 1984-85 and 1985-86 nesting seasons and the total population in the same areas. T = total numbers of crocodiles; NH = non-hatchlings; CF = correction factors for adjusting number of nests to population size.

| River | Year | Habitat | T | NH | Nests | CF T | CF NH |
|----------|------|------------------------------|-----|-----|-------|---------|----------|
| Adelaide | 1984 | Mainstream 32.0-82.0 km | 518 | 398 | 26 | 17.9 | 15.3 |
| Adelaide | 1985 | Mainstream 32.0-82.0 km | 504 | 372 | 23 | 21.9 | 16.2 |
| Finniss | 1985 | Flood plain channel no. 1 | 72 | 70 | 10 | 7.2 | 7.0 |
| Finniss | 1985 | Flood plain channel no. 2 | 70 | 70 | 3 | 23.3 | 23.3 |
| Mean | | | | | | 17.6 | 15.5 |

Table 18. The probability (p) of sighting *Crocodylus porosus* of different sizes in spotlight counts, as quantified in the Adelaide River in 1984, 13 years after protection (Bayliss et al. 1986). Sizes refer to total length estimated in feet. The correction factors (CF) are the values needed to correct counts of different sized *C. porosus* to absolute numbers.

| Size | p | CF |
|------|------|------|
| 1-2 | 0.69 | 1.44 |
| 2-3 | 0.75 | 1.34 |
| 3-4 | 0.77 | 1.30 |
| 4-5 | 0.77 | 1.31 |
| 5-6 | 0.73 | 1.36 |
| 6-7 | 0.67 | 1.49 |
| 7-8 | 0.59 | 1.71 |
| 8-9 | 0.47 | 2.13 |
| 9-10 | 0.33 | 3.08 |
| 10 + | 0.15 | 6.54 |

the numbers sighted were corrected with a single correction factor, the rate of recovery would still appear to be zero. However, if the population structure was now composed of 40 2-3', 30 4-5', 20 6-7', 10 8-9' and 5 10'+ crocodiles, the real population would be 177 $[(40 \times 1.34) + (30 \times 1.31) + (20 \times 1.49) + (10 \times 2.13) + (5 \times 6.54)]$, and there would be a positive rate of increase (+2.7% p.a.).

Because of the errors involved in estimating sizes (see above), our mean annual rates of population increase (Table 6; +8.3% p.a. for all crocodiles and +9.7% p.a. for non-hatchlings) do not account for the changed size structure. Hence the real rates of increase are higher than those given on Table 6.

6. The Adelaide River - A Test Case

Although indices derived from spotlight counts can be used to monitor trends in numbers, they are inherently inaccurate - not all crocodiles are counted. The uncounted population falls into two categories: those within the area surveyed that were not sighted (see above), for whatever reason, and those in areas associated with the mainstream that were not surveyed.

In the Adelaide River system (Fig. 15), 50 km east of Darwin, *C. porosus* occupy a variety of tidal and non-tidal habitats, some of which can be readily surveyed by spotlight and others which cannot. On Fig. 16, the total population size within the Adelaide River is estimated in stages, using appropriate correction factors for different habitats. The stages incorporated into this estimate are:

1. Spotlight counts in 1984 (CCNT, unpublished data) yielded 80 hatchlings and 514 non-hatchlings in the mainstream and its major side creeks; similar results were obtained by Messel et al. (1986, 60 hatchlings and 542 non-hatchlings; a-c on Fig. 16).
2. Using the general mainstream correction factor (1.60) between relative densities and absolute densities (Table 14), these sighted individuals give a total population estimate of 950 animals (128 hatchlings and 822 non-hatchlings). Using correction factors in Messel et al. (1981), similar numbers (95 hatchlings and 889 non-hatchlings; total = 984) are derived (d on Fig. 16).
3. However, separate correction factors are needed for upstream, downstream and side creeks (Table 14), and when these are applied to the spotlight counts, it indicates a population of 1133 individuals (e on Fig. 16).
4. Completely excluded from this estimate is the population which exists year-round in Melacca Swamp (Fig. 15), a heavily vegetated wetland which cannot be surveyed by spotlight. Using nest counts (22 in each of 1984-85 and 1985-86) as the relative density index, and correcting them with the mean correction (17.6) derived in Table 17, an additional 387 animals are indicated; this increases the total population estimate to 1520 (f on Fig. 16).
5. In addition to Melacca Swamp, the flood plains of the Adelaide River contain some 150-200 permanent and semi-permanent billabongs and minor swamps. In 1986, a sample of these was surveyed by both helicopter (106) and spotlight (20). When these indices were corrected to absolute densities, it yielded an additional 80 animals, increasing the total population estimate to 1600 (g on Fig. 16).
6. In addition to these habitats, there are large numbers of small tertiary creeks which are inaccessible to survey boats and which were not surveyed by helicopter, and additional upstream billabongs (that contain *C. porosus* and in at least one case nesting adults) which were not included in our survey. Thus 1600 represents a conservative estimate of the total population of *C. porosus* within the Adelaide River system alone.

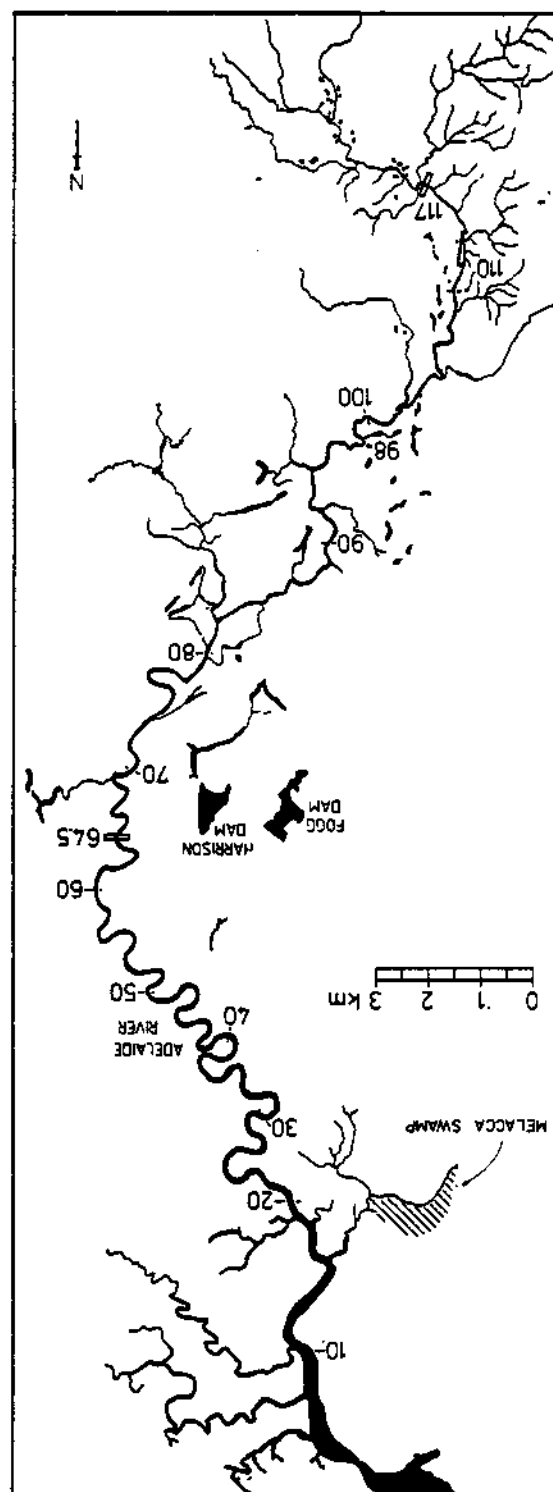


Figure 15. The Adelaide River system. Numbers are river kilometers from the mouth.

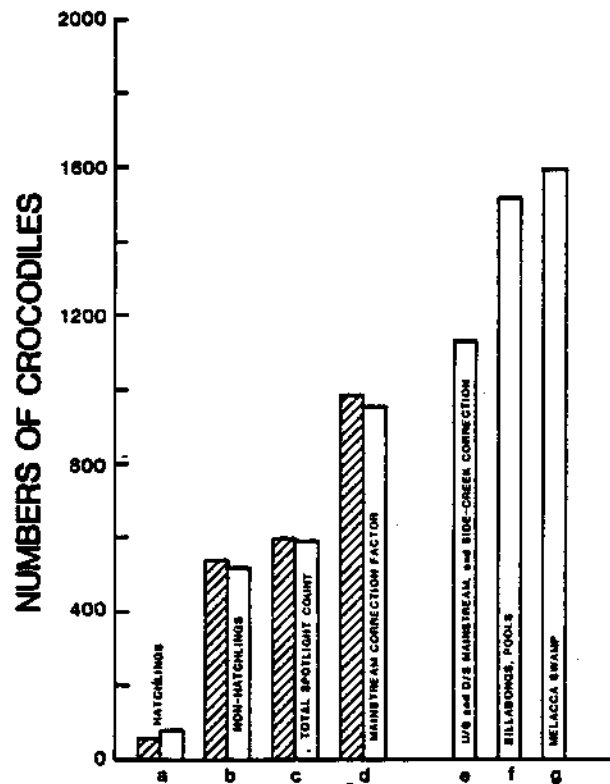


Figure 16. Number of *Crocodylus porosus* in the Adelaide River system: a, hatchlings sighted in spotlight surveys; b, non-hatchlings sighted in spotlight surveys; c, total number of *C. porosus* sighted in spotlight surveys; d, population estimate using mainstream correction factors (see text); e, population estimate using appropriate correction factors for upstream, downstream, and side creek habitats; f, population estimate accounting for *C. porosus* in various billabongs outside of the mainstream; g, total population estimate including *C. porosus* in Melacca swamp. Shaded bars indicate survey data from Messel et al. (1986), and unshaded bars are survey data from the CCNT.

THE SIZE OF THE NORTHERN TERRITORY POPULATION OF *C. POROSUS*

Webb et al. (1984) derived a conservative estimate of the Northern Territory *C. porosus* population of 30,000 individuals, and guessed that the real population was closer to 40,000 when the full extent of unsurveyed habitats was taken into consideration. This estimate was considered an overestimate by Messel (1986) and Messel et al. (1986), yet we had consistently used conservative correction factors:

1. Coastline. Two estimates of the absolute density of *C. porosus* on the coast were obtained; one between Darwin and the Victoria River (0.09/km) and one around the coast of Melville Island (0.38/km). Neither area includes the best breeding areas for *C. porosus* (Table 4), and thus a mean of the two estimates (0.24) is probably more realistic than the lower value (0.09) used by Webb et al. (1984).
2. Coastal Secondary Creeks. Coastal secondary creeks between Darwin and the Victoria River were surveyed by helicopter and the counts were corrected to absolute densities (2.57/km). The 1238 km of coastal secondary creek in the Northern Territory was composed of 638 separate creeks, with a mean length of 1.9 km, which assumes a mean total population of about 5 crocodiles per creek.
3. Major Breeding Tidal Systems. Mainstreams (1587 km) and sidecreeks (405 km; 207 creeks) were lumped in our previous estimate, and given the mean relative density of 3.16 crocodiles sighted per km derived from surveys. This was then multiplied by a conservative correction factor (1.33). The mean mainstream correction factor is closer to 1.6 (Table 12).
4. Sidecreek Corrections to Breeding Tidal Systems. In reality, the probability of sighting crocodiles in tidal sidecreeks is lower than in wide mainstreams (Table 12), and within the Adelaide River corrections for this underestimating bias increased the population by 19%. A similar correction is applicable to other major breeding systems, yet it was not used in our 1984 estimate.
5. Minor Breeding Tidal Systems. Mainstreams (3185 km) and secondary creeks (1140 km; 717 creeks) were lumped in our previous estimate, and given the mean relative density of 0.71 crocodiles sighted per km derived from surveys. This was then multiplied by a conservative correction factor (1.41). The real correction factor is probably closer to 1.6 (Table 12), plus an additional correction is needed for sidecreeks.
6. Flood Plain Creeks. In the original estimate, 1291 km of flood plain channel was given a relative density derived from spotlight counts in 10.5% of the habitat surveyed (5.60 crocodiles sighted per km). This was multiplied by a correction factor (1.56) based on results from a tidal system. The mean correction factor recently derived is 1.76 (Table 12).
7. Escarpment Channels. In the original estimate, the 534 km of flood plain channel were multiplied by a relative density of 0.60 and a correction factor of 1.53; an absolute density of 0.92 per km. Due to the physical characteristics of these channels, the correction factors applicable are probably between those of the upstream tidal areas (1.69) and those of side creeks (2.86).
8. Freshwater swamps. Although some areas of "swampland" were recognised within the Northern Territory, patches of freshwater swamp with high densities of *C. porosus* nests are more restricted (Magnusson et al. 1978). No estimate for this population was made in our original estimate, but given the numbers now estimated in Melacca Swamp alone (387 *C. porosus*), the total population within such habitats in the Northern Territory must be in the 1000's.
9. Tertiary Creeks. The 8223 tertiary creeks identified are an unknown quantity with regard to *C. porosus*. Some of these creeks are completely dry at low tide and others recede to pools. Within

major breeding tidal rivers such creeks (1256 were recognised) have a high probability of containing crocodiles, but along the coast and in low density areas they do not. No estimate was made for them.

10. The Captive Population. As of June 1986, there were 4232 *C. porosus* in captivity in Australia.

The above estimates do not account for the increase in the wild population that has occurred over the last two years, nor does it account for the many bodies of water not included on 1:100,000 maps - 30,000 to 40,000 was a conservative estimate of the *C. porosus* population in 1984.

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RADIOCESIUM LEVELS IN A POPULATION OF AMERICAN ALLIGATORS: A MODEL FOR THE STUDY OF ENVIRONMENTAL CONTAMINANTS IN FREE-LIVING CROCODILIANS

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ABSTRACT - Studies of the distribution, fate and potential impacts of environmental contaminants require a thorough knowledge of the basic ecological relationships, movements and behaviors of the target organisms. Although crocodilians have been little-studied in this regard, the continual release of radionuclides and other contaminants into elements of global circulation, suggest that even populations in remote regions, may now be significantly impacted. An example is given of a study of a population of American alligators inhabiting a reservoir which has received low-levels of radionuclide contamination from an operating nuclear production reactor. The principle radionuclide of concern was the gamma-emitter radiocesium which is known to concentrate primarily in skeletal muscle. By estimating the population number and sizes of individual alligators present in the reservoir and then determining radiocesium concentrations of selected individuals, the resident alligator population ($n = 12$), was calculated to represent an average live-weight biomass of 1.9 kg/ha, which was 3% of the total biomass/ha of all animals studied in the reservoir. When combined with previously published estimates made for other components of this same reservoir, these calculations indicated that 99% of the radiocesium resided in the abiotic components (sediments and water column). Of the radiocesium estimated to reside within the biota, only 0.4% was located within the animals, and of this fraction, only 0.5% was found in the biomass of the alligator population. Trophic-level concentration or biomagnification of radiocesium does not appear to occur in many aquatic vertebrate food webs and the few determinations that were made on alligators suggested that radiocesium concentrations in their biomass (mean = 13 pCi/g live weight) were lower than those of several of their prey species. A number of features combine to make radiocesium an ideal 'tracer' to study the principles and pathways by which many classes of environmental contaminants may cycle and become concentrated within crocodilian populations. However, more information is still needed for age-specific changes in body radiocesium contents and for rates and patterns of contaminant uptake under natural conditions.

INTRODUCTION

The catastrophic accident at the Chernobyl nuclear power station in the Soviet Union has served to underscore the potential for global environmental contamination to occur following such an event, with significant contaminant accumulation and impact occurring even in regions far removed from the source of contaminant release (Medvedev 1986). Even though many crocodilian populations are located in areas that are far removed from industrial development, they can no longer be assumed to be free of long-term chronic contaminant input from a variety of sources, as a result of global cycling pathways. While global atmospheric fallout of radioactive materials has been of particular concern in this regard (Comar 1965), the same pathways and mechanisms may also be responsible for the distribution of other classes of contaminants such as pesticides or heavy metals (Clay et al. 1974). Because of their tendency to persist in natural food webs and to cause localized cellular/tissue damage in target organisms for many years after release, many radionuclides are of special concern as environmental stressors (Table 1). Radiocesium, including the isotopes of both ^{134}Cs and ^{137}Cs , are of particular concern because of (1) its ubiquity in most environmental releases associated with both nuclear weaponry and the nuclear power industry, (2) its

Table 1. Some general properties of radionuclides which have proved important as environmental contaminants of vertebrate wildlife (adapted from Whicker and Shultz, 1982).

| Radionuclide | Physical Half-Life | Biological Retention | Principle Form of Emission | Mode of Exposure ^a | Vertebrate Target Organ | Nutrient Analogs |
|--------------------------|--------------------|----------------------|----------------------------|-------------------------------|-------------------------|------------------|
| ³ H (tritium) | 12 years | Low (days) | Beta | Ing, Abs, Ih | Total body | H |
| ¹³¹ I | 8 days | Moderate (weeks) | Beta | Ing, Abs, Ih | Thyroid | I |
| ¹³⁷ Cs | 30 years | Moderate (months) | Gamma | Ing, Abs, Ext | Whole body, muscle | K |
| ⁴⁵ Ca | 160 days | Mod.-high (wks-yrs) | Beta | Ing, Abs | Bone | Ca |
| ⁹⁰ Sr | 28 years | High (years) | Beta | Ing, Abs | Bone | Ca |
| ⁶⁰ Co | 5.2 years | Low (days) | Gamma | Ing, Abs, Ih, Ext | GI, lung, whole body | Co |
| ⁶⁵ Zn | 245 days | Mod.-high (mos-yrs) | Gamma | Ing, Abs, Ih, Ext | Liver, lung, whole body | Zn |
| ²³⁹ Pu | 24,000 years | High (years) | Alpha | Ing, Ih, Ads | Bone, lung | None |

^a Ing = ingestion, Abs = absorption, Ads = adsorption, Ih = inhalation, Ext = external gamma exposure.

relatively long half-life and thus tendency to persist in the environment for extended periods of time, (3) its tendency as a gamma-emitter to cause extensive cellular/tissue damage once incorporated into an organism's biomass, and (4) its tendency, as an analog of potassium, to accumulate in highest concentrations in skeletal muscle, which would be the tissue most likely to be consumed by man or other heterotrophic organisms in the food web.

Extensive studies by several authors (e.g., Jenkins and Fendley 1968) have shown that radiocesium and other radionuclides often tend to concentrate at unusually high levels in the bodies of free-living wildlife, following deposition as fallout from the atmospheric testing of nuclear weapons. This has been shown to be particularly true in regions of nutrient poor soils such as the arctic tundra (Hanson 1966) or the southeastern coastal plains of the United States (Jenkins and Fendley 1968). In such areas, fallout-deposited radionuclides form a relatively greater portion of the total soil nutrient pool available to the vegetation of natural communities.

The basic principles for studying the cycling and accumulation of radionuclides in the environment have been developed within the discipline known as radioecology as described by Whicker and Schultz (1982). Much of the work in this field however, has been developed on the basis of laboratory studies and has strongly emphasized homeothermic organisms, such as domestic livestock, which figure prominently in the food web of man. As pointed out by Brisbin et al. (1986), studies of contaminant cycling and radioecology have received practically no attention in the world crocodilian literature.

It is the purpose of this report to describe the basic design and preliminary results of a research program aimed at studying the uptake and cycling of radiocesium in a population of American alligators (*Alligator mississippiensis*) inhabiting a reservoir which received radionuclide releases from an operating nuclear production reactor over an extended period of time. It is also the purpose of this report to use this particular study to evaluate the approaches and methodology which might be used to study other examples of environmental contamination in other crocodilian populations throughout the world.

MATERIALS AND METHODS

This study was conducted in the Pond B reservoir (Fig. 1) located on the United States Department of Energy's Savannah River Plant (SRP). The SRP is a 750 km² nuclear production and research facility of the United States Department of Energy and is located in portions of Aiken, Allendale and Barnwell counties, South Carolina. This area has been closed to public access since 1952, providing the resident population of American alligators with freedom from poaching and many other forms of disturbance. Detailed descriptions of this site and its resident alligator population have been provided elsewhere (Murphy 1981; Brisbin 1982; Brisbin et al. 1982; Seigel et al. 1986). The Pond B reservoir forms part of the SRP's Par Pond reservoir system which has, since the early 1960's, provided a closed-loop system of cooling water for one or more of the SRP's nuclear production reactors. Pond B was formed in 1961 by impounding a natural stream water course, while at the same time diverting water to the impoundment from the site's R-reactor complex. Input from the R-reactor was discontinued in 1964 and since that time hydrologic input to the reservoir has been only from direct rainfall and subsurface groundwater seepage. Although the surface area and other physical characteristics of the reservoir vary slightly in response to balances of precipitation and evaporation, the lake is approximately 87 ha in surface area and has 9.0 km of shoreline. Maximum depth near the dam is 12.2 m. The lake has numerous shallow coves which are heavily vegetated with macrophytes in contrast to the more open deeper waters in the central part of the lake. The majority of the lake's alligators are generally found within 10-20 m of the shore in the shallower more vegetated areas (Fig. 1).

Between 1960-1964, the heated effluents from the R-reactor were contaminated with varying amounts of several radionuclides which resulted from direct inputs from the reactor itself and leakage from a faulty fuel element stored at the reactor site (Alberts et al. 1979). Radionuclide inputs to Pond B

POND B

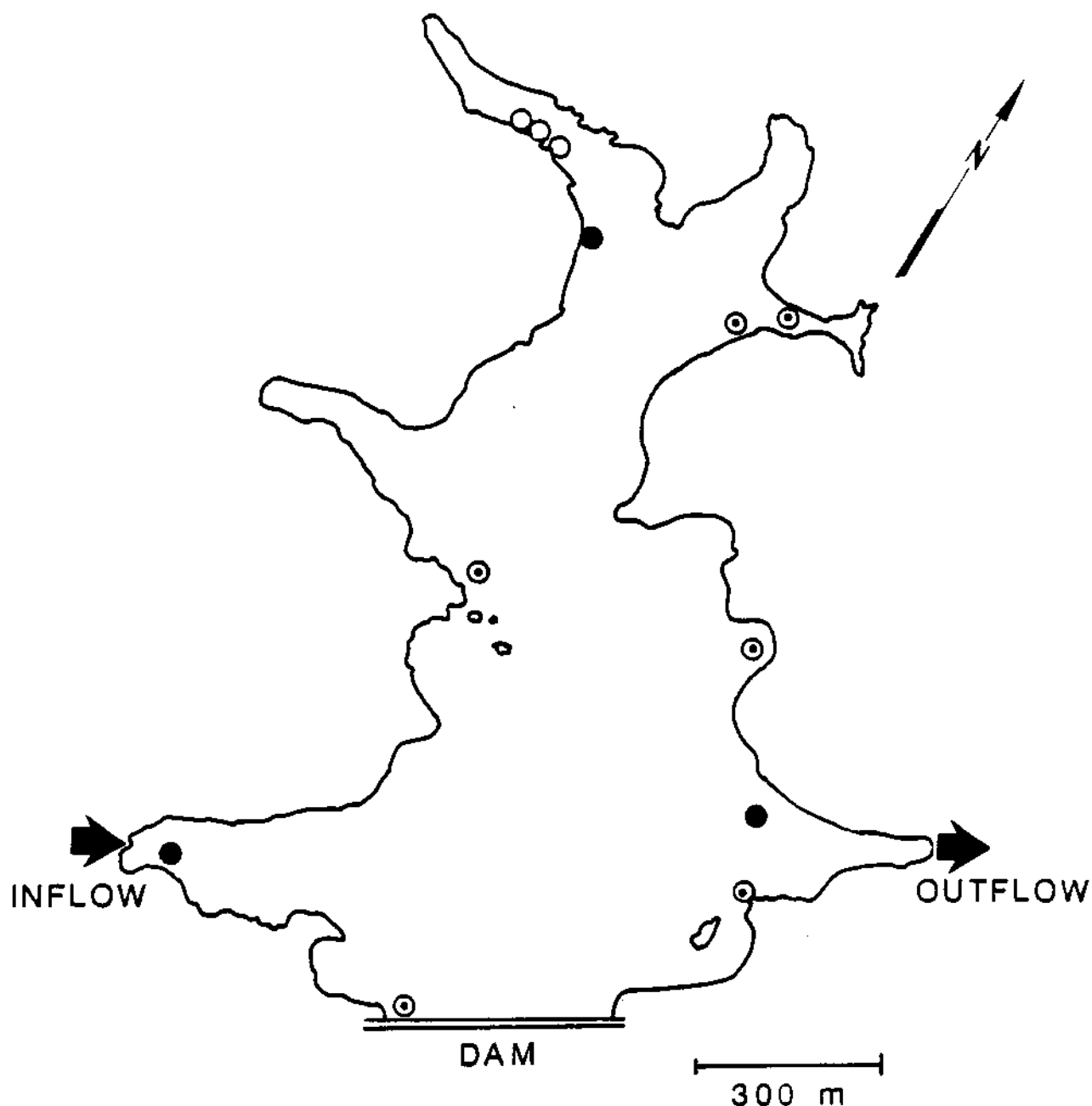


Figure 1. Diagrammatic representation of locations of alligators identified as inhabiting the Pond B reservoir on the U.S. Department of Energy's Savannah River Plant. Symbols are placed at locations approximating the geographic center of all sightings of that individual (total sightings = 46). Further details concerning the alligators indicated here are provided in Table 2. Solid circles = adults (> 1.7 m), open circles with central points = immatures (0.5 - 1.6 m), and open circles = juveniles (< 0.5 m). Solid arrows indicate locations where reactor effluents entered and exited the reservoir between 1961-1964.

during this period totaled about 50,000 Ci of tritium, 150 Ci of ^{137}Cs , 12 Ci each of ^{90}Sr , and $^{103,106}\text{Ru}$ and lesser amounts of ^{60}Co , $^{238,239}\text{Pu}$ and other transuranic elements.

Measurable quantities of most of these radionuclides, particularly radiocesium, can still be found in both abiotic and biotic components of the Pond B reservoir ecosystem. Since the time of reservoir formation, the waters of Pond B have tended to become nutrient-poor and relatively acidic, as is typical for natural freshwater systems of this region. This in turn has tended to produce a situation favoring high concentration factors (concentration in biota/concentration in water) for radiocesium (Whicker et al. 1984). This, in combination with the generally low cation-binding capacity of the soils and sediments of region (Brisbin et al. 1974a; Whicker et al. 1984), has tended to enhance the continued recycling of radiocesium and other radionuclides into the biotic components of the reservoir.

Murphy (1981) described the alligator population resident in Pond B in the late 1970's as including several adults of breeding size. Although no evidence of reproduction was found at that time, Murphy predicted that the subsequent reproduction of these animals together with the likely dispersal of juvenile alligators to Pond B along the canal connecting it to the main portion of Par Pond (Fig. 1) should eventually result in the establishment of a viable breeding population of alligators in this reservoir.

Population numbers of alligators were estimated in the present study by night-time eye-shine census techniques (Wood et al. 1985). Census cruises were made from an airboat with the entire shoreline of the reservoir being covered each night that a census was conducted. Shorelines were censused from a distance of approximately 50 m although the size of the reservoir permitted the identification of even juvenile alligators at a distance greater than the maximum width of the reservoir. Census cruises, which took approximately 1.0 hrs to complete, were conducted on June 16, 17, 18, July 17, 18, 19, August 5 and September 17, 1986. Each alligator that was located was approached as closely as possible in order to allow estimation of body size. Very small animals were captured whenever possible and marked with tail scute clippings in order to prevent duplicate identifications of the same individuals. Following the last census cruise, records from all cruises were combined in order to estimate the maximum number of individuals that were likely to be present in the reservoir. In this procedure, locations of alligators on different cruises were compared with respect to body size and location in the reservoir. A strong tendency was shown for most animals to be associated with specific locations along the shoreline, thus facilitating the differentiation of individuals and preventing duplicate counting. Body size estimates, expressed as total body length to the nearest meter, were converted to body weight estimates using length-weight regression equations presented by Chabreck and Joanen (1979).

Body-burdens of radiocesium were determined by procedures similar to those described by Brisbin et al. (1973). In the present case, body burdens were determined for hatchling alligators in a lead-shielded whole-body counting chamber with a NaI (Th) crystal measuring 10.2 cm in height and 15.2 cm in width. Hatchlings were restrained in plastic tubes and placed so that the center of their body was centered immediately above the crystal detector. Gamma emissions were analyzed on a Canberra 8100 multi-channel pulse-height analyzer, and counts accumulated during a 2000 sec counting period were compared with same-day net counts from an aqueous phantom of similar body size and configuration to the alligator. Body burdens of radiocesium were expressed as pCi/g of whole-body live weight. Although no alligators have yet been captured which could not be counted in the previously described equipment, the determination of radiocesium contents for larger individuals (> 1.5 m) would require either sacrifice and whole-body homogenization techniques (Brisbin and Smith 1975) or, if alligators were to be kept alive after radiocesium determination, alternative counting techniques could be adapted using portable field gamma-counting equipment similar to that described by Rabon and Johnson (1973) and Wright and Splichal (1973) for use with deer and feral swine. In using this field equipment, the thick skin of large alligators would require the use of correction equations described by Stribling et al. (1986).

RESULTS

The eight census cruises produced a total of 42 sightings of alligators (range = 3-9 sightings/cruise). An additional four sightings were made between census cruises while conducting other research activities at the reservoir. Of the 46 sightings, 34 were able to provide a size estimate for the alligator observed. Eight of the sightings included the hand-capture and positive identification of one of three hatchlings found in a cove at the northern end of the reservoir (Fig. 1). These hatchlings were always found in close proximity to one another and probably represented a cohort which hatched from a nest in that area in 1985.

Taken together, the census cruise data indicated that in addition to the three hatchlings, nine other alligators resided in the Pond B reservoir, including three adults whose sizes suggested that they were potentially reproductive (Table 2, Fig. 1). Application of length-weight regression equations indicated that these alligators represented a total estimated biomass of 161.2 kg, or an average of 1.85 kg/ha for the entire reservoir.

Whole-body burdens of radiocesium for the three hatchling alligators, as determined on June 17 and 18, 1986, were 12.68, 15.33 and 11.61 (mean = 13.21) pCi/g live weight. Applying this value to the total alligator biomass estimated for the reservoir indicated a total inventory of 0.0244 Ci radiocesium/ha for the Pond B alligator population. This value was then combined with previously published radiocesium inventory estimates for other biotic and abiotic compartments of the reservoir, and with preliminary inventory data recently collected for waterfowl (principally American coots (*Fulica americana*) and ring-necked ducks (*Aythya collaris*), and largemouth bass (*Micropterus salmoides*) (Table 3). These comparisons indicated that less than 0.6% of the total inventory of radiocesium present in Pond B was found in the biota. Approximately 99% of the radiocesium was found in the sediments, with most of the remainder being in the water column of the reservoir. Of the radiocesium found in the biota, 99.6% was incorporated into the biomass of the macrophytes (Table 3). Of the total inventory of 3.9 Ci radiocesium/ha found in the animals, only 0.5% was incorporated into alligator biomass. The inventory of radiocesium in the alligators was lower than that of any other biotic component studied, although it was of the same general order of magnitude as estimated for benthic gastropods and waterfowl. The radiocesium inventory in the alligators was nearly two orders of magnitude less than that found in the largemouth bass and benthic invertebrate community of the reservoir.

DISCUSSION

The present status of the Pond B alligator population, as determined by the census reported here, is a reasonable consequence of the status reported by Murphy (1981) who found 3-11 alligators, including several large adults, in Pond B in the early-mid 1970's. Since these earlier surveys, there have been several known deaths of large adult alligators in Pond B (Murphy 1981; Brisbin et al. 1982; Seigel et al. 1986), possibly as a consequence of *Aeromonas hydrophila* infections and stress (Brisbin 1982). These, together with the probable dispersal of juveniles into Pond B from the adjacent North Arm of Par Pond, as predicted by Murphy (1981), would produce a population age structure similar to that found in this study (Table 2).

As illustrated by the study reported here, there are a number of quantities which are difficult to estimate accurately in the process of calculating the total standing crop of a contaminant such as radiocesium in a population of wild crocodilians. Errors in estimating these quantities will undoubtedly introduce errors of varying magnitude into the final inventory calculations and hence may influence the final conclusions which are drawn. Chief among these factors is the difficulty involved in capturing and accurately estimating the average radiocesium body burdens of large adult crocodilians. In fact, no such estimates have yet been obtained for the Pond B alligator population, and all estimates of biomass radiocesium concentrations thus

Table 2. American alligators censused during the summer of 1986 on the Pond B reservoir of the U.S. Department of Energy's Savannah River Plant.

| Alligator No. ^a | Estimated Total Length (m) | Estimated Live Body Weight (kg) ^b |
|----------------------------|----------------------------|--|
| 1 | 2.40 | 55.90 |
| 2 | 1.45 | 9.90 |
| 3 | 1.70 | 17.50 |
| 4 | 0.36 | 0.10 |
| 5 | 0.37 | 0.11 |
| 6 | 0.24 | 0.08 |
| 7 | 1.12 | 3.60 |
| 8 | 1.00 | 1.30 |
| 9 | 1.25 | 5.60 |
| 10 | 2.40 | 55.90 |
| 11 | 1.25 | 5.60 |
| 12 | 1.25 | 5.60 |
| | | Total = 161.20 |

^a Alligators are numbered in sequence, according to their location along the reservoir shoreline, proceeding clockwise from the point of reactor effluent inflow, as indicated in Fig. 1.

^b Calculated from the length/weight regression equation for wild alligators (Chabreck and Joanen 1979).

had to be based on the average of those values obtained for the more easily captured and handled hatchlings. Since alligators shift their diet from a largely insect/invertebrate to a vertebrate prey base as they grow larger, there is the possibility that weight-specific radiocesium body burdens may change with age. However, as will be discussed later, data from other species such as fish-eating birds (Brisbin et al. 1973; Dombay and McFarlane 1978) and snakes feeding on aquatic vertebrates (Brisbin et al. 1974b) from this same reservoir system, indicate that predators in the higher trophic levels of vertebrate food webs do not tend to show high levels of radiocesium biomagnification. Thus, radiocesium concentration levels in the biomass of the larger adult alligators is probably not significantly greater and possibly could even be lower than those reported here for the hatchlings.

Another possible source of inaccuracy in the calculation of contaminant standing crop is the field estimation of the sizes of individual animals, and the use of correct regression coefficients to predict body weights from field estimates of length. Murphy (1981) has shown significant differences between the growth patterns of alligators inhabiting different regions of the Par Pond reservoir system, and if these differences produce corresponding differences in length-weight relationships, the validity of using length-weight regression coefficients derived from populations in another part of the species range (e.g., Chabreck and Joanen 1979) must be questioned until verification can be obtained with actual length-weight data from individuals from the Pond B population itself.

While certain quantities in a contaminant inventory calculation may be more difficult to estimate for crocodilians than other species, others may actually be easier. Estimation of alligator numbers, for example, particularly in a situation such as Pond B, can almost certainly be performed more accurately than can the estimation of population numbers for such biota as fish or benthic invertebrates. The population estimate of 5434 for largemouth bass in Pond B, for example, was based on 747 mark-recaptures and had a 95% confidence interval of 3589-7279 individuals. In terms of the average weight/individual bass (mean = 255 g), this represents a deviation of about 470 kg for the total bass population biomass. This is more than twice the total biomass estimate for the entire reservoir population of either alligators or waterfowl (Table 3).

Despite the factors discussed above, it is unlikely that any of the inaccuracies involved in estimating the inventory/distribution of radiocesium in the Pond B alligators would alter the basic conclusion of this study -- namely, that concentration levels of this isotope in alligator biomass are relatively low compared to many other species and/or compartments in the reservoir (Table 3), and that, above all, the total amount of released radiocesium which is now contained in the alligators is infinitesimally small (Table 3). To be sure, population densities of alligators in Pond B (mean = 0.47/mi of shoreline censused) are low compared to some other alligator populations whose densities can range as high as 64 alligators/mi elsewhere in South Carolina (Bara 1974) or 58/mi in Florida (mean for all states = 5.25-5.64/mi in 1978 and 1977, respectively; Chabreck 1979). However, even if the alligator population density, and hence total standing-crop biomass, were increased 100-fold to approximate the highest densities reported in the literature, the alligators would still represent less than 0.3% of the radiocesium inventory in the biota and less than 0.001% of the total inventory in the reservoir. Moreover, the calculations presented here for the percentage contribution of alligators to the Pond B radiocesium inventory (Table 3) are likely to represent an overestimation since no data were available for several biotic components of the reservoir--notably turtles and fish other than largemouth bass. The radiocesium inventory in the reservoir's catfish (*Osteichthyes: Ictaluridae*) may be a particularly important omission in this regard.

These findings emphasize the importance of concomitant ecosystem studies of physical factors such as the chemistry of the sediment/water interface, for understanding of the distribution, fate and effects of such released contaminants. However, while physical forces may indeed be of overwhelming importance in determining the rates and patterns of radiocesium distribution within the reservoir, the importance of that small part of the total inventory which does indeed come to contaminate wildlife such as alligators, should not be underestimated. As an endangered species, many legal issues presently relate to the state of well-being of alligators in the southeastern United States. Thus it is extremely important, and in some cases legally mandated, to evaluate those factors which regulate the fate and effects of such contaminants in these

animals—even though, in terms of the total ecosystem and/or biota, the total amount of contaminant involved may be relatively minor. Indeed, the rise of environmental consciousness in the United States and much of the developed world, was often first focused by concerns over contaminant levels in just such predators at higher trophic levels of the ecosystem. Levels of pesticide residues in birds of prey and fish-eating seabirds, for example, have always been one of the foremost causes of environmental concern since the first publication and societal impact of *Silent Spring* (Carson 1962).

It cannot be emphasized too strongly, however, that any study of the ecological cycling of radionuclides or any other environmental contaminant in a population of alligators or other legally or politically 'visible' species must include consideration of contaminant distribution and movement within all biotic and abiotic compartments of the ecosystem. In the case of the Pond B alligator population, for example, this means that, in addition to studies of sediment and water chemistry, radiocesium cycling must also be studied in the populations of fish, turtles, waterfowl, and other species that may form an important part of the alligators' food base. Previous studies by Brisbin et al. (1973) have shown that American coots contain the highest body burdens of radiocesium of any of the common species of waterfowl found in the Pond B reservoir, and since they are extremely abundant, and relatively slow moving, these coots may form an important item in the diet of resident alligators. Coots arrive in the Par Pond reservoir system in October and depart for northern breeding grounds the following spring. During their winter stay on the reservoir, these birds increase in radiocesium content until December, January and February. Thereafter, a precipitous decline in radiocesium content occurs as the birds which had been resident at the site move northward and are replaced by birds that had wintered further south and thus had not had an opportunity to accumulate elevated body burdens of radiocesium. Thus, the intake of radiocesium by alligators feeding on these waterfowl would be greatest in the mid-winter months—a period of time when most alligators are probably least likely to be feeding actively because of cold temperatures. However, as indicated by Murphy (1981) the input of heated reactor effluents into parts of the Par Pond reservoir system has created a condition in which some resident alligators may indeed remain active and feed, as confirmed by field observations, even during the coldest winter months. This in turn, would expose alligators to the intake of radiocesium from feeding on coots, at the time of year when the radiocesium content of these birds was highest. In the Pond B reservoir, however, the lack of such thermal input would probably prevent such an occurrence since few if any of the alligators remain active and feeding during the colder months (Brisbin et al. 1982).

The inventory approach to contaminant distribution in an ecosystem such as Pond B, is based upon the structure of the ecological pyramid of standing-crop biomass and ultimately the contaminant itself, in various trophic levels. In terms of kg of biomass/ha, the biomass pyramid of Pond B (Table 3) is similar to several of those described by Odum (1971) for a variety of both aquatic and terrestrial ecosystems. As mentioned previously, however, the principle of biomagnification of the contaminant through successively higher trophic levels does not seem to hold for the Pond B ecosystem. The highest weight-specific radiocesium concentrations are shown by macrophytes and several of the potential prey species of alligators (invertebrates, bass and waterfowl; Table 3).

Besides the inventory approach, a complete understanding of contaminant distribution and cycling requires a knowledge of turnover rates within both populations and the bodies of individual organisms. While no such studies have yet been performed with crocodilians, studies of bioelimination rates of radiocesium in captive snakes (Staton and Brisbin 1974) agree well with calculations reported by Reichle et al. (1970) for other poikilothermic vertebrates. Together, these predict that radiocesium half-lives of alligators of larger body size (> 2 m) would probably be extremely long, and complete elimination of the isotope following cessation of contaminant input, might require several years or longer. Such 'physiological' turnover rates as described by these authors and determined under laboratory conditions, may differ significantly from 'ecological' turnover rates which quantify the rates of elimination under free-living field conditions. As shown by Bagshaw and Brisbin (1984) these ecological turnover rates may be as much as 6-8 times longer than laboratory-determined physiological turnover rates for the same species. Studies of contaminant turnover rates under field conditions, however, are often difficult to undertake since they require the multiple recapture, whole-body counting and release of given individuals (Fendley et al. 1977).

Table 3. Standing crop inventories of biomass and radiocesium contents of American alligators and other components of the Pond B reservoir of the U.S. Department of Energy's Savannah River Plant^a.

| Components | kg/ha ^b | Average pCi Radiocesium/g ^b | Ci Radiocesium/ ha | References |
|------------------------------------|---------------------|---|-------------------------|---|
| <u>Abiotic Components:</u> | | | | |
| Sediments ^c | --- | 1,450 ^d | 199,000 | Whicker et al. (1986), J. E. Pinder (pers. com.) |
| Filtered Water | 37,000,000 | 0.020 | $\frac{740}{199,740}$ | Whicker et al. (1984) |
| | | Total = | | |
| Seston: | 799 ^e | 46.1 ^e | 36.8 | Whicker et al. (1984), and J. Bowling (pers. com.) |
| <u>Flora:</u> | | | | |
| Aquatic Macrophytes | 6,568 ^e | 144 ^e | 945 | Whicker et al. (1986) J. E. Pinder (pers. com.) |
| <u>Fauna:</u> | | | | |
| Benthic Invertebrates ^f | 26.2 ^e | 47.5 ^e | 1.24 | Whicker et al. (1984) |
| Benthic Gastropods ^g | 9.64 | 5.00 | 0.0482 | Whicker et al. (1984) |
| Largemouth Bass ^h | 15.9 ⁱ | 161.0 ^j | 2.56 | i, j (see below) |
| Waterfowl | 1.24 ^{k,l} | 39.8 ^m | 0.0494 | k, l, m (see below) |
| Alligators | 1.85 | 13.2 | $\frac{0.0244}{0.0244}$ | This Study (Table 2) |
| Totals = | 54.8 | | 3.92 | |

- a Calculated on the basis of radiocesium estimated to be present in 1983-85 (Whicker et al. 1986).
- b Expressed as live (wet) weight.
- c Cores taken to a depth at which radiocesium levels were no longer detectable.
- d pCi/cm^2 of bottom surface area.
- e Assuming a ratio of 0.25 g dry weight/g live (wet) weight for all biomass.
- f Excluding gastropods.
- g Soft tissue plus shell.
- h Fish ≥ 150 mm standard length.
- i Assuming a population size of 5434 fish as estimated in the summer of 1986 (G. C. White, pers. com.) and an average live weight of 255.1 g/fish ($n = 747$, R. Buchner, pers. com.).
- j Average for 28 fish sampled from Pond B in 1983 (F. W. Whicker, pers. com.).
- k Based on population estimates by Mayer et al. (1986) and assuming a ratio of coots to other waterfowl species of 0.71, as estimated by Brisbin (1974) for the North Arm of the adjacent Par Pond reservoir.
- l Based on a weighted average, combining average live body weights for coots (mean = 535.7 g, $n = 10$) and Ring-necked Ducks (mean = 681.5 g, $n = 10$) collected from the Par Pond reservoir (R. A. Kennamer, pers. com.).
- m Based on a weighted average, combining average radiocesium body burdens determined for coots (mean = 54.1 pCi/g live weight, $n = 6$) and Ring-necked Ducks (mean = 12.8 pCi/g live weight, $n = 5$) collected from Pond B in 1984 (F. W. Whicker, pers. com.).

The ease with which individual hatchling alligators could be repeatedly located, recaptured and whole-body counted without apparent undue stress or harm suggests that these may be among the most appropriate of all organisms in Pond B for studies of radiocesium turnover rates under field conditions.

The general principles established by the Pond B alligator study have application for studies of many forms of environmental contaminants besides radionuclides. Studies by Clay et al. (1974), have indicated, for example, how studies of radiocesium in waterfowl can provide a better understanding of the contamination of the same birds with heavy metals. However, only gamma-emitting radioisotopes such as radiocesium can be easily quantified in whole-body biomass without sacrificing and/or tissue biopsy procedures. Such gamma-emitters are thus ideal for testing hypotheses concerning cycling and uptake rates in individual organisms as described above.

Finally, regardless of whatever contaminant may be involved, the ultimate interest of contaminant-cycling studies to those charged with the conservation and well-being of wildlife, involves the possibility of direct harm or damage to those organisms in whose bodies the contaminant may come to reside. To date, there has been no evidence of either somatic or genetic damage to any of the alligators or other organisms studied in Pond B. However, the potential for increased levels of environmental contamination as the result of possible future accidents and/or other inadvertent releases of radionuclides on either a local or global scale, suggests strongly that even though contamination levels may presently be low and apparently inconsequential to the organisms involved, studies of the patterns of ecological distribution and cycling dynamics of contaminants in such ecosystems can be important to the future well-being of many forms of wildlife in general and crocodilians in particular.

ACKNOWLEDGEMENTS

Studies of the Pond B alligator population were supported by a contract (DE-AC09-76SROO-819) between the Institute of Ecology at the University of Georgia and the United States Department of Energy. Assistance in field studies was provided by Susan McDowell, Howard Zippler, Rick Buchner, Greg Kreikemeir and Amanda Corey. Laura Brandt and Frank Mazzotti also provided helpful advice. John Pinder, F. Ward Whicker and John Bowling provided data on radiocesium levels in various components of the Pond B reservoir system, and along with Mark Staton, Richard Seigel and James Knight, provided critical readings of the manuscript.

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PREDATION OF ALLIGATOR NESTS IN OKEFENOKEE SWAMP NATIONAL WILDLIFE REFUGE, GEORGIA, U.S.A.

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ABSTRACT - Predation of 70 alligator nests in Chesser and Grand Prairies of the Okefenokee Swamp is discussed. In 11 nesting seasons 16% of monitored nests survived predation. Black bears (*Ursus americanus*) and raccoons (*Procyon lotor*) were the major consumers of alligator eggs. Thirty-nine percent of female alligators guarded their nests from human intrusion and 58% of these nests survived predation.

INTRODUCTION

Across its range the American alligator (*Alligator mississippiensis*) exhibits some degree of nest tending behavior but predators of alligator eggs still manage to significantly affect nesting success. In coastal South Carolina raccoons destroyed 11.1% of 117 clutches late in the incubation period (Wilkinson 1983). On Rockefeller Refuge, Louisiana, Joanen (1969) reported a 16.5% (N = 44) loss of nests to raccoons and found that predation occurred usually at the end of the seventh week of incubation with raccoons making multiple visits to the nest mound until all eggs were consumed. In a North Florida study 43% of 35 nests were preyed upon primarily by raccoons (Deitz and Hines 1980). The highest recorded predation rate was in the Okefenokee Swamp National Wildlife Refuge, Georgia, where predators destroyed 86% of nests (Metzen 1977). Here I report on nest predation and identify predators in the Okefenokee Swamp.

METHODS

The study area of Chesser and Grand Prairies is an aquatic macrophyte marsh containing thousands of tree islands. A boat trail connects the prairies with several fishing lakes and in normal rainfall years is navigable by motor-boat traffic. Twelve km of this boat trail and its intersecting alligator trails were explored for nests. Searches for nests were conducted on foot or from paddle craft.

To identify predators of eggs, some nests were monitored with set cameras; Kodak Instamatic X-15 cameras with mouse-trap shutter releases were mounted on stakes and connected to the nest mound with thread. Disturbance to the mound tripped the camera and a single photograph recorded each incident. Unless the integrity of the mound was disturbed by predators, eggs and egg chambers were not examined.

When possible, nesting females were identified by atypical scutes. The nest guarding behavior of females was determined by approaching their nests; those hissing or lunging at the intruder were considered to be guarding nests; those present but not displaying defensive behavior toward humans, were considered not to be guarding nests. "Guarding" as defined here does not necessarily mean that females avoiding humans will not guard nests from other predators.

RESULTS

Eighty-eight percent of nesting starts occurred from 20 June to 30 June. In 11 nesting seasons (1976-1986) 83 nests were located within 200 m of the 12 km trail through Chesser and Grand Prairie; predators destroyed 70 nests (Fig. 1). Fifty-nine percent of all nests and 42% of nests monitored with cameras were preyed upon before 10 July. Because of this early predator activity 45% of nests in Grand Prairie and 39% in Chesser Prairie were first discovered after predation.

Nest sites - Typically, nests were constructed in the interior of small (< 100 sq m) tree islands or at the periphery of large (> 100 sq m) tree islands. On large tree islands, nests were often at the base of a tree. Two or more alligator trails connected nests with holes, ponds or boat trails. Twenty-one nests in Chesser Prairie were located within 3 m of boat trails or ponds more than 1 m in depth and these deep-water nests had a predation rate of 67%.

Guarding Behavior - Nests of alligators not guarding from humans had higher predation rates than nests of guarding alligators. In Grand Prairie only one nest was guarded and predators destroyed all except one nest. In Chesser Prairie 44% of nests were unguarded with a predation rate of 86%; guarded nests had a predation rate of 39%. Although male alligators (> 3 m in total length) were frequently observed near females nesting in deep water, only two were observed in possible guarding postures: one hissed at me near a nest which had been preyed on and the other lunged and hissed at me near a pod of two day old neonates.

Nest repair - After predations some damaged nests still contained viable eggs; often a small excavation exposed the upper eggs with the mound retaining most of its mass and shape. In 17% (N = 12) of nests preyed on before 10 July, females made effective repairs. During this early incubation period all nesting females crawled over their nests and used their feet to scoop more plant material over nest mounds. Thus, the same activity that added mass to undamaged nests also repaired nests damaged by predators. Repeated or major structural damage to nests was not usually repaired but on 6 July, 1978 a female in Grand Prairie scooped a small amount of nest material over two whole eggs after her other eggs had been consumed in repeated predations. During nest repair she used her mouth to remove whole egg shells from the mound; set cameras photographed two other females engaged in similar behavior. Nests which had been emptied of viable eggs by predators usually contained a few scattered egg shells but some apparently intact nest mounds contained whole egg shells in the egg chamber.

Predators of eggs - Set camera photographs identified predators in 16 incidents of nest predation. One nest was destroyed by rice rats (*Oryzomys palustris*), two by raccoons, four by raccoons and bears, and nine by bears.

Early in the nesting season bears, including sows with cubs, were commonly seen wading in shallow water near nests. Although alligators were not observed defending nests from bears, one set camera photographed an egg consuming bear with extensive neck wounds. Bears usually consumed all eggs during a single visit but sometimes they made repeated visits to mounds.

In Grand Prairie a nest damaged in daylight hours by a bear, was repaired by the alligator then further damaged by raccoons and bears on three successive nights until all eggs were consumed. Bears sometimes left whole egg shells at the nest site but usually only small fragments of shell remained. Typically, nest mounds damaged by bear were massively excavated and leveled to the depth of the egg chamber.

Before the beginning of the nesting season, raccoons excavated holes in old nest debris and they preyed on nests throughout the incubation period. Set camera photographs identified raccoons excavating nests and consuming eggs during both night and daylight hours. Typically they excavated holes into the egg chamber and drained eggs by removing one end of the egg. Usually eggs were not consumed in one visit

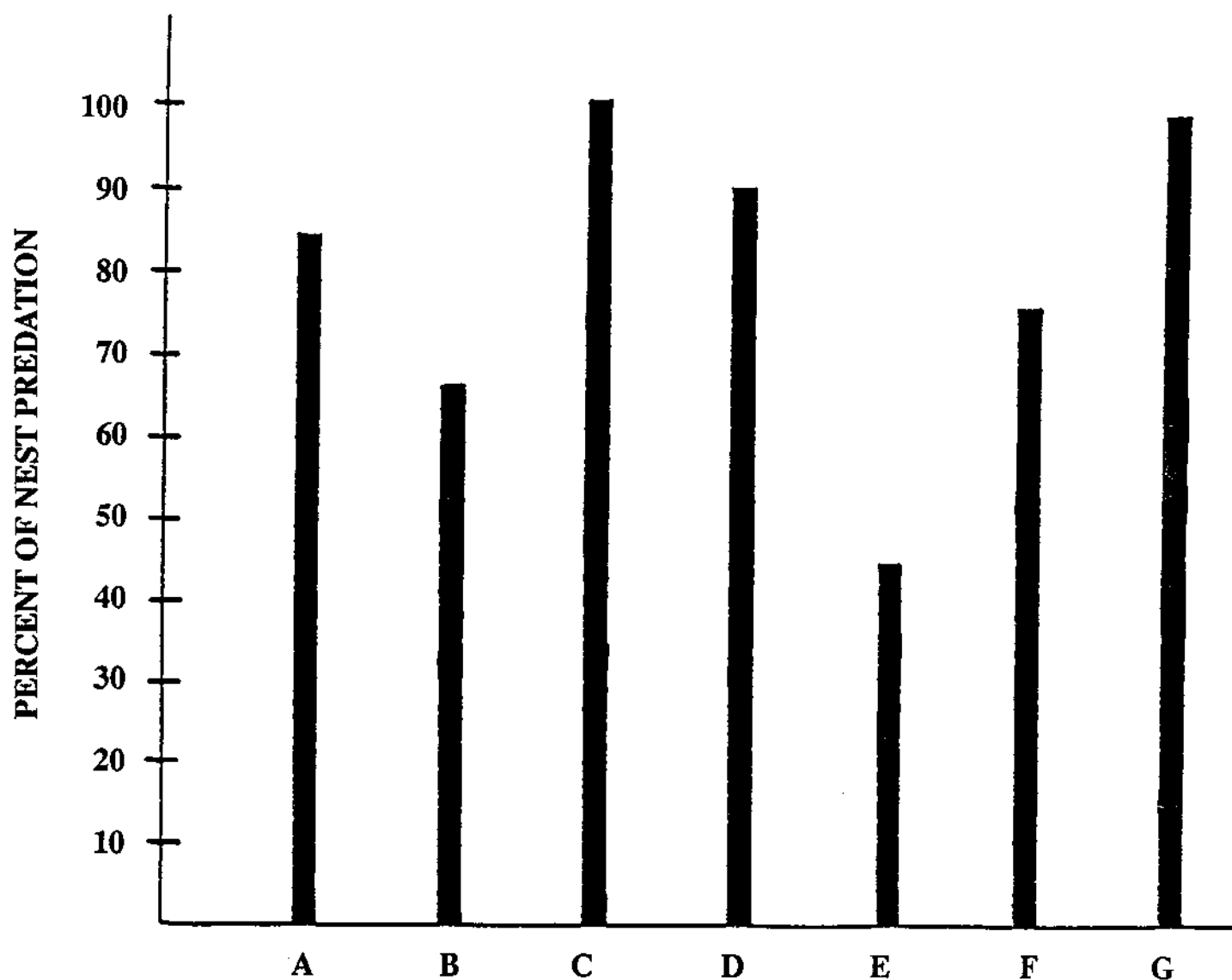


Figure 1. Predation rates of nests in Okefenokee Swamp, Georgia. A = nests with turtle eggs; B = nests near deep water; C = repaired nests; D = unguarded nests; E = guarded nests; F = Chesser Prairie; G = Grand Prairie. Total predation rate of 70 nests = 84%.

and raccoons returned over a period of several days to consume the remainder of the alligator eggs. Raccoons also consumed turtle eggs in the mound.

Turtles often laid eggs in alligator nests and in the process they eroded the mound, cracked alligator eggs and exposed alligator eggs to sunlight and opportunistic predators. Seventeen percent of alligator nests contained one or more clutches of turtle eggs and had a predation rate of 83%. Set camera photographs taken before 10 July identified Florida red-belly turtles (*Chrysemys nelsoni*) on alligator nests during night and daylight hours. One alligator nest was damaged by *C. nelsoni* laying eggs on 26 and 27 June and 3 July, 1986; the turtles deposited eggs inside the egg cavity exposing several alligator eggs and on 4 and 6 July, rice rats bit through the shells of the exposed eggs. By 29 July all alligator and turtle eggs in this nest were destroyed.

Nesting alligators, including those not guarding nests from humans, attacked turtles crawling on their mounds. On one occasion an alligator lunged with open mouth at the gravid turtle; another nesting alligator bit an escaping *C. nelsoni* but did not crush the turtle's shell.

DISCUSSION

Black bears were responsible for the massive and early nest predation in the Okefenokee Swamp. At the shallow-water nesting sites they could easily evade female alligators defending their nests. Although only two male alligators were observed in defensive postures near nest sites, it is possible that the movement of large territorial males in the vicinity of deep-water nests inhibited bear activity. Deep water might also be an advantage for females defending nests from bears. It has been suggested that alligators see humans as facsimiles of bears (Deitz and Hines 1980) and that an alligator guarding a nest from humans will also guard from bears. Guarding alligators were more successful in hatching nests and presumably more successful in thwarting predators of eggs, but some non-guarding alligators evidently defended nests from bears; because bears usually consumed all eggs in one visit it was assumed that an alligator was defending her nest from bears when the bear made several visits to consume all eggs. A Florida study showed that guarding alligators immediately attacked small predator models but delayed serious attack on large predator models (Kushlan and Kushlan 1980). Humans and bears are the only predators able to seriously threaten the nesting alligator. For a female alligator an adult black bear is a formidable opponent and if her nest defense requires contact with the bear she could be injured. Such aggressive contact could also alter her behavior in successive encounters with bears and perhaps with humans. Guarding alligators that are attacked or stressed by humans learn not to guard (Kushlan and Kushlan 1980) and sometimes a single incident can produce this behavior (Joanen and McNease 1970). Nesting alligators encounters with aggressive bears could have the same effect. It is also possible that the bears which massively prey on nests in Grand Prairie have had such extensive nest raiding experience that few alligators can thwart their egg consuming habit.

In defense of nests from raccoons, alligators seem to differ in behavior. In Louisiana an alligator was present at her nest but did not defend it from a raccoon (Joanen 1969). In Florida an alligator not defending her nest from humans did defend from a raccoon (Deitz and Hines 1980).

Raccoons are not a lethal threat to an adult alligator and can not usually consume all eggs in one visit, but they are successful in preying on nests. In the Okefenokee some raccoons learn to raid nests from their mothers - set cameras identified females with young preying on alligator eggs. Other raccoons probably follow familiar scents to nest mounds. Raccoons inexperienced in locating alligator eggs but experienced in locating turtle eggs by scent could be expected to occasionally cross an alligator mound and find both the familiar turtle eggs and the unfamiliar alligator eggs.

Turtles laying eggs in nest mounds can affect predation of alligator eggs. In Florida, turtles have damaged alligator nests, excavating the mound, crushing eggs and depositing a powerful scent package for predators to locate (Deitz and Jackson 1979, Kushlan and Kushlan 1980). Certainly, exposure of alligator eggs by turtles makes the eggs vulnerable to opportunistic predation. In a South Carolina study, 4.2% of alligator nests were used by rodents with no impact on eggs (Wilkinson 1983). In my study, however, after *C. nelsoni* damaged one nest the exposed eggs were destroyed by rice rats.

Turtles crawling on a nest mound might be easily thwarted by the guarding alligator. Dietz and Jackson (1979) reported two gravid, dead *C. nelsoni* near nest mounds but the heavy shell of *C. nelsoni* in Okefenokee has an excellent chance of withstanding the pressure of a female alligator's jaws and turtles can employ other escape strategies, such as burrowing into the mound or assuming a stationary posture when confronted by the guarding alligator.

Nests with minor damage were effectively repaired by some Okefenokee alligators; mounds were restored and exposed eggs were reburied. Repair behavior should be an advantage to alligators nesting in areas of intense predator activity but because nests can be targeted again by the same predator and because other predators can be attracted to the scent of broken eggs these nests remain extremely vulnerable to predation. In this study, predators eventually destroyed all repaired nests.

ACKNOWLEDGEMENTS

I thank past Okefenokee National Wildlife Refuge Manager John Eadie, and present Manager John Schroer and staff for their cooperation and courtesy. Atlanta Zoological Society provided grants for this study.

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CLASSIFICATION AND POPULATION STATUS OF THE AMERICAN ALLIGATOR

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The Endangered Species Act of 1973 required that the U.S. Fish and Wildlife Service categorize the American alligator (*Alligator mississippiensis*) into three basic classifications throughout its range in the southeastern United States: endangered, threatened, or threatened due to similarity of appearance [T (S/A)]. These categories simply designate the general population status of the animal in relation to its rate of recovery. Generally, the endangered status indicates a low population within a geographic area; whereas, the threatened status indicates an increasing population well on its way toward recovery. Threatened due to similarity of appearance indicates a recovered population. Important factors which are considered in making a status determination include: habitat evaluations; government research, management, and enforcement programs; natural mortality factors; utilization; the adequacy of regulatory mechanisms; and miscellaneous other factors.

Alligators are currently classified as threatened in 5.8 percent of their range, as endangered in 48.9 percent of their range, and as recovered in 45.3 percent of their range (Table I). The historic stronghold of the alligator is for practical purposes the 51.1 percent of the range presently classified as threatened S/A (recovered) or threatened. Classification status reviews are periodically conducted by the U. S. Fish and Wildlife Service, usually as a result of state petitions to change the legal status of the alligator. The collection of biological information pertaining to status reviews has greatly enhanced management capability for the alligator.

Since the IUCN/CSG meeting in Caracas, Venezuela in 1984, the U. S. Fish and Wildlife Service reclassified the biological status of the alligator in only one state. The entire State of Florida was reclassified to threatened S/A, effectively returning management authority back to the State (Federal Register Vol. 50, No. 119, 20 June 1985).

Most recently, a rangewide delisting for the American alligator has been proposed (Federal Register Vol. 51, No. 105, 2 June 1986). A final rule, if approved, will consolidate the classification status of all American alligators, throughout the range, to the special category of threatened due to similarity of appearance. This historic action formally recognizes that the population status of the alligator is indeed in great shape.

POPULATION STATUS BY STATE

Ten states contain alligators in all or parts of the state. In general, alligator populations are increasing throughout the range. Areas on the fringes of the range generally have stable populations and cannot biologically harbor high densities, characteristic of states bordering the Gulf of Mexico.

Louisiana - The 1985 coastal marsh population, where nest count indices were used to calculate population levels, was projected to be 468,000, a 14.1% increase over the estimate for 1984. Water levels affect the degree of nesting, a factor which must be considered when making annual population estimates based on nest transects (McNease and Joanen 1978). Nest count estimates have shown an annual increment of approximately 10.1 percent since initiation of the survey in 1970 (Joanen et al. 1984). In areas of the state where the nest count method is not feasible, standardized night counts were conducted along established

transect lines. Night count data were then applied to population modeling. Louisiana personnel surveyed 23 different areas of the state in 1985; transects covered a total distance of 127 miles. Alligators per mile averaged 6.4, slightly below the range-wide average of 7.06 for the same year (Chabreck 1986). McNease and Joanen (1978) reported available alligator habitat within Louisiana coastal marshes comprise 2.9 million acres; Taylor (1980) reported statewide alligator habitat for non-marsh as 1.1 million acres.

Florida - Florida population trend monitoring is limited to annual night-light surveys run on selected areas scattered throughout the state. Seventeen areas were surveyed in both 1984 and 1985; 8 showed increases and 9 decreases. Mean alligators per mile counted along all survey routes was 16.3 in 1984 and 16.5 in 1985. However, water levels were lower in most parts of the state in 1985 (A. Woodward, pers. comm. 1986). Alligator night count data collected prior to 1977 and compared to night count information collected between 1977-81 show increases in numbers of alligators observed per mile. Florida lakes averaged 11.9 alligators per mile prior to 1977 and 13.8 per mile from 1977-81. In comparison, Florida marshes averaged 11.3 per mile prior to 1977 and 13.3 per mile from 1977-81 (Federal Register Vol. 49, No. 120, 20 June 1984).

Georgia - A 1986 alligator population survey indicated population increases are occurring in most of Georgia. An analysis of population trends by counties showed that 64 were increasing, 39 were stable, and none were decreasing. The 1986 estimates increased from 1% to as high as 5% when compared to the 1984 survey. A total of 2,17,701 acres of alligator habitat was reported in a 103 county area (S. Ruckel, pers. comm. 1986). Georgia personnel surveyed 12 different areas of the state in 1986, transecting a total distance of 77.8 miles. Alligators per mile averaged 13.25, well above the range-wide average of 7.06 in 1985 (Chabreck 1986).

Texas - Texas alligator population trends, in general, remain stable to increasing. Aerial nest counts in coastal counties indicate an estimated population of over 150,000 alligators occurring on the middle and upper coast. Additionally, sizable populations exist in the extensive inland alligator habitat; however, the relative magnitude of this inland population remains to be determined. Night count surveys in 1986, covering 196 miles, indicated an average of 4.08 alligators per mile. The coastal marsh of Jefferson County exhibited the highest population trend data with a high of 70 alligators per mile. Average density in the 220,000 acres of upper coastal marsh as measured by 1985 and 1986 aerial nest counts was 61 alligators per 100 acres.

Relative abundance of alligators as measured by frequency of sightings in 80 Texas counties within the historic alligator range in Texas varies from regular sightings in 46% of the counties to occasional sightings in 25% of the counties to rare sightings in 23% of the counties. In those same counties over the past five years, biologists estimate that alligator populations are increasing in 33% of the counties, decreasing in 16%, and unchanged in 37%. Population trends were unknown in 14% of the counties. Changes in Texas alligator habitat since 1984 are not measurable. Some coastal marsh continues to be lost to subsidence, draining, and spoil activity, while reservoir construction has created additional inland habitat (B. Thompson, pers. comm. 1986).

South Carolina - Eight South Carolina counties (29%) were reported to have increasing populations out of 28 counties containing alligators. Increases were estimated to be 2-5 percent. Nineteen counties (68%) reported stable populations (T. Murphy, pers. comm. 1986). The best habitat is associated with coastal impoundments and marshes, comprising approximately 100,000 acres in Georgetown, Charleston, Colleton, and Beaufort Counties. The next tier of counties inland represent moderate to high alligator densities and a significant amount of habitat, particularly in Berkeley and Jasper Counties. The amount of suitable alligator habitat diminishes rapidly from these counties to the fall line, with generally isolated ponds supporting limited numbers of alligators. South Carolina reports approximately 250,000 acres of alligator habitat statewide (T. Murphy, pers. comm. 1982). Most nesting (84%) occurred in seven river drainages. The drainages in order of highest nest counts were: Santee, Cooper, Combahee, Savannah, Ashepoo, Pee Dee, and South Edisto Rivers (Wilkinson 1983).

Arkansas - The alligator's range is limited in Arkansas. The trend for Arkansas alligators is a stable to slightly increasing population. Since 1972, the state restocked 2,700 alligators from Louisiana in 40 of 45 counties lying within the historic range of the species. Because of the restocking effort, successful reproduction has been documented in 6 counties that were previously void of alligators (S. Barkley, pers. comm. 1986). Night count data for 13 miles of survey lines searched in 1986 indicate 0.08 alligators per mile (Chabreck 1986).

Mississippi - No current population estimates are available for this state. Mississippi night count data for 54.0 miles of survey lines indicate an average of 1.46 alligators per mile, well below the range-wide 1986 average of 7.06 alligators per mile (Chabreck 1986). However, this data compares closely with its neighboring state of Alabama which recorded 1.76 alligators per mile.

Alabama - No current population estimates are available for Alabama. Seven night count routes, covering 134.5 miles in length, were run which averaged 3.49 alligators per mile (Chabreck 1986). However, of the 7 surveys conducted, 4 were run in the coastal county of Baldwin which is known for its high alligator population. Excluding this one county, alligators per mile of survey averaged 1.76; comparable with Mississippi findings.

North Carolina - Alligators occurred in low densities on night count survey routes in coastal North Carolina. Highest densities occurred in estuaries of the Cape Fear #3 Watershed and in lakes of the Neuse Watershed. Alligators were found to be concentrated on military bases, national forests, and private property. Alligator densities decreased by watershed from south to north. No alligators were found north of Albemarle Sound, supporting the belief that this is the northern limit of the alligator's range. There are no recent night count data from survey routes in North Carolina. However, the sampling design which was established in 1979-80, is for the express purpose of providing baseline data with which to compare the results of future surveys. Now that North Carolina has a non-game and endangered wildlife program, it is hoped that their surveys can be repeated at 3-5 year intervals, so as to monitor population trends (P. Doerr, pers. comm. 1984).

PROPOSED STATUS CHANGE

The U. S. Fish and Wildlife Service proposed to classify the American alligator throughout its range to the status of threatened due to similarity of appearance, under provisions of the Endangered Species Act. The proposal as advertised in the Federal Register (Vol. 51, No. 105, 2 June 1986) deals with alligator populations in Alabama, Arkansas, Georgia, Mississippi, North Carolina, Oklahoma, and South Carolina. Alligator populations in these seven states are relatively stable and contain approximately 17 percent of the species' total habitat. This action formally recognizes that the alligator is no longer biologically threatened or endangered but supports a need for continued federal control on taking and commerce to insure against excessive taking and to continue necessary protections for the crocodile (*Crocodylus acutus*) in the United States (Federal Register Vol. 51, No. 105, 2 June 1986).

AVAILABLE ALLIGATOR HABITAT

Noticeable increases in alligator populations range-wide have stimulated state conservation departments to evaluate these populations and also to classify alligator habitat (McNease and Joanen 1978, Joanen and McNease 1981, Taylor 1980, Thompson et al. 1983, Wilkinson 1983, Federal Register Vol. 49, No. 120, 20 June 1984). Obvious differences exist in the quality of habitat for alligators and in most cases habitat has been classified into 3 distinct habitat types: coastal marshes, inland freshwater rivers, swamps and marshes, and natural and man-made lakes. Surveys have shown that alligator populations vary according to habitat type and also that within a single habitat type obvious differences may exist in population levels. McNease and

Joanen (1978) found that certain ecological features may exist in one type that may not exist in the same habitat type just a few miles away. In the coastal marshes of Louisiana, interspersions of land/water ratios and also water levels were two important factors that must be taken into consideration when evaluating alligator habitat. Probably the best example of this in Louisiana are some dense solid stands of *Panicum hemitomon* which provide little or no open water, no habitat diversity, and very poor alligator nesting habitat. However, other *Panicum* marshes interspersed with ponds, potholes, and open lakes provide some of the finest nesting habitat to be found on the Louisiana coast.

Inland lakes, both man-made and natural, possess varying degrees of alligator populations. Important factors that must be considered when evaluating these areas as alligator habitat are vegetative cover and water depth. Lakes which seem to provide the best alligator habitat are those which have some open freshwater marshes attached, or those which have vegetative cover extending from the shoreline out into the open water areas.

Freshwater swamps attached to large river systems or lakes probably provide the largest single habitat type within the range of the alligator; however, they possess the lowest alligator concentrations when compared to the other habitat types. The exception to this would be swamps which possess imbedded open freshwater marshes of sizeable acreage. Generally, riverine swamps lack the proper interspersions of vegetative cover and land/water ratio of the coastal marsh zone or inland lakes. Riverine systems are also known for their extremes in seasonal water level fluctuations along with extreme currents.

The amount of alligator habitat (wetlands) reported by 5 states are presented in Table 2. Although any wetland habitat has the potential of being used by alligators, the frequency of use varies considerably. Salt water marshes, large deep open water lakes, and large rivers in Louisiana have been found to be used only occasionally and only by the adult segment of the population. A careful review of the different habitat types along with a better understanding of their value to alligators is of the utmost importance in the management of a resource. Wetlands in themselves do not qualify as alligator habitat, but rather the true estimate of habitat suitability must be measured by studying wetlands which possess distinctive ecological features and comparing these characteristic ecological features to existing alligator populations.

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TABLE 1. Alligator Classification Status by State - September 1986

| State | Number of Counties | | | Total |
|----------------|--------------------|------------|------------|-------|
| | Threatened S/A | Endangered | Threatened | |
| Mississippi | | 55 | | 55 |
| Alabama | | 33 | | 33 |
| North Carolina | | 21 | | 21 |
| Texas | 74 | | | 74 |
| Arkansas | | 3 | | 3 |
| Oklahoma | | 1 | | 1 |
| Georgia | | 81 | 21 | 102 |
| Louisiana | 63 | | | 63 |
| Florida | 64 | | | 64 |
| South Carolina | | 23 | 5 | 28 |
| Total | 201 | 217 | 26 | 444 |
| Percent | 45.3 | 48.9 | 5.8 | |

TABLE 2. Available Alligator Habitat Reported for Five States

| State | Habitat Type | Acreage |
|----------------|----------------------------------|-----------|
| Louisiana | Coastal marsh | 2,900,000 |
| | Inland wetland* | 1,100,000 |
| Florida | Fresh marsh | 3,600,000 |
| | Permanently flooded wooded swamp | 1,200,000 |
| | Lakes | 1,700,000 |
| | Rivers and streams | 200,000 |
| South Carolina | Coastal marshes and impoundments | 100,000 |
| | Inland wetland* | 150,000 |
| Texas | Coastal marsh | 293,000 |
| | Inland wetland* | 3,328,000 |
| Georgia | Unclassified wetland | 5,824,000 |

* Swamps, lakes, ponds, rivers and streams, marshes, reservoirs.

FEED FORMULATION FOR ALLIGATORS: AN OVERVIEW AND INITIAL STUDIES

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The feeding of alligators (*Alligator mississippiensis*) by means of a nutritionally balanced pelletized feed, produced with conventional feed ingredients and feed mill technology, would offer many advantages to the alligator farming industry. Such a product could be prepared in numerous locations and at any time of the year, thus improving upon the current practice of relying on locally and/or seasonally available feed such as animal carcasses, fish, and/or meat scraps. Expenses and operating problems associated with freezer storage could be avoided. The mixing of vitamins, trace minerals, and feed additives could be done more accurately and thoroughly through the use of modern feed mill technology than is currently practiced. Most importantly, the nutrient content of the food and the nutrition of the alligators, could be more effectively controlled.

Managing the nutrition of any animal requires a fair understanding of the nutritional needs and versatility of the species in question. Unfortunately, information on the nutrient requirements of alligators is scanty at best, and the ability of alligators to utilize nutrients in practical feedstuffs has received practically no attention. Pilot studies have indicated that alligators can grow on rations composed of practical feed ingredients (T. Joanen, L. McNease, M. Staton, unpubl.). Growth, however, was slower and with poorer feed conversion than for alligators fed a diet of nutria (*Myocastor coypu*) carcass, a conventional feed source for alligator farming in the United States. Further studies aimed at making practical feed formulation a reality in the alligator industry have now been initiated. The objectives are: (1) to formulate a practical, cost-effective ration for the feeding of alligators in farming operations, (2) to determine the most effective and practical physical form in which to use such a ration, and (3) to develop a feeding program making optimal use of the ration. In order to meet these goals, a number of basic issues must be considered, as discussed below.

THE NUTRIENT REQUIREMENTS OF ALLIGATORS

The basic nutrient groups in the diet of any species are proteins, carbohydrates, lipids, vitamins, and minerals. These nutrients must provide the energy and raw material required by the organism for maintenance, growth, and/or reproduction. Energy is mainly derived from carbohydrates, protein, and lipids, whereas the nutrient classes which contribute to the structural needs of the organism are mainly proteins, minerals, and lipids. It is important to note that the composition of these nutrient classes (e.g., amino acids in proteins, fatty acids in lipids, specific vitamins or minerals, etc.) may be just as important as

the total amount of each of the nutrient classes in the total ration. Furthermore, the ratio of the nutrient classes or nutrients to each other is a major consideration. For example, the protein:energy ratio and the calcium:phosphorus ratio are known to be key nutritional characteristics of the diets of those species that have been sufficiently studied. Required nutrients must be identified and the minimum, optimum, and maximum amount of each required nutrient must be established. Possible interactions between nutrients must also be considered.

It is possible that some nutrient requirements and interactions among nutrients can be reasonably anticipated for alligators from data on other species. Of special interest are the carnivorous fishes because of their similar dietary habits and poikilothermic nature.

Finally, it should be noted that, as for other species, the nutrient requirements of alligators will change with age and season. For example, using data from Coulson and Hernandez (1983), it can be estimated that the weight-specific metabolic rate of alligators decreases approximately tenfold from the time of hatching until reaching harvest age. These same authors demonstrated that blood glucose levels of alligators change seasonally, even when the animals were maintained at a constant temperature. Such variations in blood glucose may affect appetite and food consumption, and it may be necessary to vary the nutrient content of the food during periods differing in consumption patterns.

The following discussion describes the major dietary components in relation to what is known concerning the nutrient requirements of alligators.

1. Carbohydrates - Coulson and Hernandez (1983) correctly point out that alligators, like all other extant crocodilians, are carnivores and that ingestion of plant carbohydrates in the natural environment is minimal for this species. This may occur, for example, while consuming prey to which plants have adhered or in which undigested plants remain in the gastrointestinal tract. Coulson and Hernandez (1983) also point out that of a number of carbohydrates fed experimentally to caimans (*Caiman crocodilus crocodilus*), only glucose was absorbed with other monosaccharides, disaccharides and polysaccharides being unassimilated. (Furthermore, as will be discussed later, Coulson and Hernandez (1983) reported that alligators were unable to utilize protein of plant origin). These conclusions appear logical because of the carnivorous habits of crocodilians.

The apparent inability of crocodilians to utilize carbohydrates and proteins of plant origin led to the general avoidance of grains and other feedstuffs of plant origin in attempts at feed formulation for alligators. Obviously, it would be wasteful to include ingredients which could not be utilized in a diet. Nevertheless, from a practical standpoint, it would be highly desirable to include some carbohydrate in crocodilian rations. Carbohydrates are considered to be the least expensive energy source in practical livestock rations, and they possess binding properties which make them highly desirable in manufacturing various forms of pelletized rations, such as semi-moist petfoods (e.g., Drochner and Muller-Schlosser 1980). This is especially important to alligators since their jaw structure makes it unlikely that they can efficiently use a meal form of diet. Furthermore, when feeding alligators, it is likely that some of the feed would be dragged into water or perhaps even be fed to the animals in water as a routine practice. The presence of a good binder would prevent the feed from readily dissolving and thus enhance its utility. It would be most desirable to use a binder which could also serve as a nutrient source.

It is noteworthy that other carnivorous species, such as salmonid fish and cats, are able to utilize dietary plant carbohydrate in formulated feeds (e.g., NRC 1978; Spannhoff and Plantikow 1983). For example, although there is no known dietary carbohydrate requirement for the domestic cat, commercial cat foods containing 40% or more are well utilized (NRC 1978). Carbohydrate utilization may not be as efficient in carnivores as in omnivores. However, it is sufficient to allow inclusion of carbohydrates in amounts which contribute significantly to energy content and binding characteristics of such feeds.

It is known that the utilization of carbohydrate by normally-carnivorous species is enhanced by heat-treatment, a common process in feed-manufacturing. Such heat treatment may enhance the nutrient value

of ingredients containing carbohydrate for alligator feed formulation as well. It is also known that increasing the complexity of dietary carbohydrates has a negative effect on its availability to carnivorous species (Spannhof and Plantikow 1983). Hence, if alligator feeds are to include carbohydrate, care will necessarily need to be taken in including them.

2. Protein - As carnivores, alligators undoubtedly have the ability to metabolize large quantities of dietary animal protein. Beyond the basic requirement of dietary protein for maintenance, growth, and (as adults) for reproduction, protein is either excreted or broken down to carbon skeletons and converted to glucose/glycogen or lipid for storage. Feeding protein above the maintenance, growth, and reproductive requirements is wasteful. This is of particular practical interest since protein is the most expensive component of formulated rations, and therefore, calories supplied by protein are more expensive than those from carbohydrates or fat. It is thus essential in cost-effective feed formulation for alligators to determine the amount and amino acid composition of dietary protein which will optimally meet requirements, and meet the requirements for energy and glucose with feed-grade fats and carbohydrates when ever possible.

A major question to be answered in alligator protein nutrition is the feeding value of proteins of plant origin. It has been reported that alligators are unable to digest proteins of vegetable origin (Coulson and Hernandez 1983). As with carbohydrates, this seems plausible due to the carnivorous feeding habits of this species. However, other carnivorous species such as cats, dogs, and salmonid fish are readily able to utilize plant protein. Because protein sources of vegetable origin are frequently less expensive than animal by-products, because there are many more feed ingredients of plant origin, and because plant-based proteins may contain amino acids in abundance which are lacking in protein sources of animal origin, it would be highly desirable to add feedstuffs of vegetable origins to the list of ingredients available to the alligator feed formulator. This topic deserves further research.

3. Lipids - Coulson and Hernandez (1983) point out that dietary fat is readily digested by alligators. It is probable that alligators have a basic dietary requirement for lipid, at least for a source of glycerol and essential fatty acids. In fact, alligators grow well on rations low in fat, and those grown on some high fat diets may develop a "fatty liver" condition (Coulson, pers. comm.). From a management standpoint, it is also important to keep fat at low levels in the diet, since fat from food dragged into water may make cleaning and sanitation of tanks in which alligators are grown more difficult (T. Joanen, pers. comm.).

From the standpoint of cost, it would be desirable to include as much fat in the diet as possible, within the constraints listed above and assuming that it is efficiently used by the animal and that it does not present a problem in manufacturing the food. A less expensive energy source such as fat should be used, whenever possible, to spare the use of more expensive protein. It is interesting to note that another carnivorous species, the domestic cat, has been known to utilize over 60% dietary fat under experimental conditions (NRC 1978). Such levels could not be considered in practical diets for a number of reasons, but it does suggest that the metabolism of at least some carnivorous species are well adapted to high levels of dietary fat.

Perhaps even more important than the amount of fat is the composition of fat fed to animals, particularly carnivorous species. Carnivores frequently receive adequate essential fatty acid levels in their natural diet, and some species lose the ability to synthesize the essential metabolites (e.g., for cats, see Rivers et al. 1975; Rivers and Frankel 1980). Essential fatty acid deficiencies are most likely to occur in animals maintained over long periods of time. Since alligators are routinely farmed for up to three years, essential fatty acid nutrition must be addressed. Very importantly, Garnett (1985) has recently suggested that *Crocodylus porosus* requires a dietary source of long chain polyunsaturated ω 3 fatty acids. Garnett (1985) cites reports that crocodiles fed over extended periods of time on pork meat develop a dermatitis of unknown etiology, which could result from an essential fatty acid deficiency. Thus addition of some long-chain polyunsaturated ω 3 and/or ω 6 fatty acids to alligator rations at some level may be vital. It is interesting to note that Halver (1976) considers the fatty acid composition of dietary fat to rank second only to amino acid composition in terms of importance in formulating diets for cultivated warmwater and coldwater fish species.

4. Vitamins - The vitamin needs of alligators have been the subject of some concern and research. Lance (1982) and Lance et al. (1983) have discussed the importance of Vitamin E in alligator reproductive performance. Coulson and Hernandez (1983) point out that a dietary source of vitamin D or exposure to sunlight for several hours a day is needed to allow for normal bone formation.

A vitamin premix currently available to alligator farmers (McNease and Joanen 1981) has been used successfully for a number of years. The recommended usage level of this premix is 0.5 to 1% by weight, when added to meat rations such as nutria, chicken, or fish. It is important to point out that such meat rations consist of as much as 50 to 75% water. Thus, the premix is actually being fed at levels of 1 to 4% on a dry matter basis. This represents an excessive range in utilization which is probably counter-productive from a cost standpoint. Other questions also arise concerning the differences between using this premix in a dry ration rather than with a meat. For example, what is the difference between the endogenous vitamin content of the meats being fed and that of rations composed of practical feedstuffs? What contribution do gut microflora make to the overall vitamin requirement of the animal? Are vitamins from the premix utilized equally when fed with a "wet feed" (i.e., meat) as with a formulated feed?

Pilot studies and experimental work reported here have used the vitamin premix at 1% of diet, but this diet, as formulated, consisted primarily of dry matter (less than 10% water by analysis). This is a considerably lower rate of vitamin supplementation than is currently used with fresh meat. It is not known to what extent these differences may have influenced results to date.

5. Minerals - Lance (1982) and Lance et al. (1983) have studied the role of some trace minerals in alligator reproduction. However, the trace mineral nutrition of growing alligators has received little attention in the literature. The minimum and maximum levels of minerals of both micro- and macronutrient status must be considered. Until specific studies are available, reasonable guidelines can be drawn from two sources: (1) the mineral content of common prey items in the natural environment, and (2) the mineral requirements of other animals, particularly carnivores. Neither of these approaches is without problems however. As will be discussed subsequently, for example, the amounts of calcium and phosphorus in the diet, even at levels substantially below those present in nutria carcass, significantly affect consumption and growth performance of alligators offered diets containing differing amounts of these minerals.

Use of a trace mineral premix, as currently added to rations for other domestic species, may be advisable until the mineral requirements of alligators have been further studied. We have included a trace mineral premix in diets of the second experiment reported here, and it is possible that its use resulted in the improved food conversion ratios, as will be discussed later.

FEEDSTUFFS AVAILABLE FOR PRACTICAL FEED FORMULATION

The availability of a long and diverse list of ingredients is desirable for feed formulation purposes. Currently, the list of ingredients available to the alligator feed formulator must be restricted to feedstuffs of animal origin (e.g., Table 1). Grains and other ingredients of plant origin are not included because it is presumed that they would not be effectively utilized by alligators, as discussed previously.

Expansion of this list would be an important contribution to the practice of alligator feed formulation. Casein, an animal-based ingredient is excluded from Table 1 because of its relatively high cost. However, it may be useful in small quantities, since it is an excellent protein source and offers some binding characteristics. Casein has been used in experiments described herein, and apparently is well utilized.

It should be noted that the availability of nutrients in any feed is not equal to the gross levels present. Such availability varies according to species, ingredient, nutrient, and the presence of other ingredients in

the diet. Nutrient availability is a subject which should receive considerable attention as the practice of alligator feed formulation becomes widespread.

PRACTICAL RATIONS AND THEIR USE IN THE ALLIGATOR INDUSTRY

Alligators are apparently able to utilize diets with high levels of dietary protein (e.g., nutria meat contains approximately 70% protein). However their ability to use dietary carbohydrate and fat, as noted above, is in question. The percentage of protein could perhaps be lowered by increasing fat and carbohydrate levels, as allowable by nutritional, managerial, and manufacturing constraints. Nevertheless, a high protein diet of at least 50-60% appears probable. The dietary protein requirement of the young of many fish species, for example, exceeds 50% (NRC 1983). Such high protein diets are amenable to pelletizing by the extrusion process, which is currently used in manufacturing feed for crayfish, fish, and other aquatic species. Once the amount and composition of fat and carbohydrate, if any, that can be added to the diet and efficiently used by alligators have been resolved, the overall level of the major nutrient classes in the diet can be fixed. With regard to the specific composition of nutrient classes, the mineral content of the diet and the fatty acid composition of dietary lipid appear to be the issues still most in question. Past experience, the results of studies to date, and experiments planned for the near future would appear to be sufficient to suggest working vitamin and amino acid compositions for a commercially viable product which would be useful to the alligator industry.

FACILITIES FOR THE STUDY OF ALLIGATOR NUTRITION

Special facilities were constructed to allow controlled, captive studies of alligators through their first 12 months of life. Housed in an insulated building, sixteen tanks, constructed of plywood and lined with fiberglass, were laid out in four rows of four tanks each. The tanks were raised on supports such that they were approximately thirty inches from floor level.

Each row consists of four rectangular tanks providing a total living area of 10 to 12 square feet (0.9 to 1.1 square meters) per tank. This living area was apportioned into a dry area (1.3 of area) and a wet area (2.3 of area), with water levels ranging from 4 to 8 cm.

Beneath each row was a reservoir for water which was recirculated through the four tanks. Water in the reservoirs was heated with a 1500 watt heating element to a temperature which was controlled by a thermostat with a remote sensor submerged in the water. A pump, placed in the reservoir, was operated by a clock-controlled switch. Warm water was pumped to the alligator tanks on a regular basis. A return line carried overflow water back to the heating reservoir. The temperature of the water in which the alligators were located was set and maintained relatively constant by adjusting the thermostat. The frequency of pump operation varied according to the room temperature, ranging from 10 to 18 intervals (20 minutes each per 24 hours) including periods when room air temperature fell as low as 3.9°C. This arrangement was successful in maintaining temperatures generally between 26° and 32°C a great percentage of the time, and averaging approximately 29.5°C (see experimental section for data). Water temperature was monitored by a thermometer submerged in the water of each tank.

PRELIMINARY STUDIES

The following two experiments have used the facilities described above to provide preliminary data relevant to the development of a feed for alligator farming.

I. FEEDING TRIALS TO EVALUATE THE EFFECTS OF SUPPLEMENTING A DRY FORMULATED FEED WITH VARIOUS ADDITIVES.

Introduction

Since the natural diet of alligators consists of a relatively large proportion of protein, we initially focused on this aspect of the diet. Preliminary analyses (Table 2) indicated that nutria meat was approximately 70% protein, on a dry matter basis. Just as important, however, was the amino acid composition of the protein to be fed. The amino acid composition of diets used in this study were arrived at by targeting the amino acid balance of: (1) nutria, (2) alligator eggs, (3) fish muscle (following the "balanced amino acid mixture" of Coulson and Hernandez (1983)), since alligators are known to grow well on diets of fish (McNease and Joanen 1981), and (4) chicken egg, which is considered to be a protein of high nutritional value for a wide variety of vertebrates. An attempt was made to formulate the feed such that the amino acid composition, as a percentage of protein, matched at the least the minimum for the same amino acid in one of these four proteins. The calculated amino acid composition of this diet (designated as "basal") is compared with that of these reference protein sources in Table 3. In most cases, the targeted minimum amino acid level was exceeded, and only in the case of tryptophan was the level less.

The basal diet (Diet 1-1), was then modified by the addition of a number of nutrients in order to assess the effects of their supplementation (Table 4). Lysine and methionine were selected because they are generally considered to be the first and second limiting amino acids in the rations of traditional livestock species, and because synthetic forms of these amino acids are commercially available at prices and in quantities which make their inclusion in livestock rations routine practice. Lysine (80%) was added at 2% of diet (Diet 1-2), and DL-methionine at 1% (Diet 1-3). Diet 1-4 consisted of both 2% additional lysine and 1% additional methionine above their respective levels in the basal ration.

Calcium and phosphorus are generally maintained proportional to each other in formulated rations and hence are discussed together here. The levels of these minerals in the basal diet exceeded the requirements for all other species during their pre-adult growth period, and in fact, exceeded the amounts normally found in commercial rations, raising the possibility that high levels of these minerals might be having deleterious effects on food utilization and growth performance. For example, it is well known that high calcium levels lead to decreased food consumption and growth in broiler chickens (Scott et al. 1982). Furthermore, high levels of calcium may have an inhibitory effect on energy utilization (e.g., Cheng et al. 1949). For this reason, three additional diets were formulated. These three diets started with Diet 1-4 as the control, and contained added Ca/P (Diet 1-5), added fat (poultry oil) (Diet 1-6), or both (Diet 1-7).

Methods and Materials

Hatchling alligators were obtained from Rockefeller Wildlife Refuge in Louisiana 2 to 4 weeks after being hatched by artificial incubation. Body weight variation was considerable, varying from 49 to 117 g at the time the experiments were begun, approximately 4 to 6 weeks after hatching. Therefore, the animals were separated according to size rank, into two blocks of "small" (avg. = 76.6 g) and "large" (avg. = 95.2 g) animals. Thirteen small animals and 10 large animals were then assigned to each of two tanks (see

description of facilities, above). The two tanks were then randomly assigned to 8 treatments representing experimental and control diets.

Water temperatures ranged between 25.1° and 31.9°C, averaging 28.4°-30.0°C for all tanks. Room air temperatures varied from 8.9° to 28.8°C, while air temperatures within the tank were much more constant, ranging from 25.0° to 30.0°C (mean = 27.4°C, $n = 16$). Tanks were cleaned twice per week, after feedings. Water in the heating reservoirs was changed and the reservoirs cleaned approximately every two weeks. During the brief period when the tanks were being cleaned, alligators were exposed to room air temperatures.

Alligators were fed 3 times per week. Food offered, on a wet-weight basis, represented 25% of the average body weight on a weekly basis, i.e., 8.33% per feeding. For formulated diets, "wet weight basis" meant a 50:50 mix of the formulated diet and water. Since nutria meat contained significantly more than 50% water (62.6 to 76.0%, $x = 70.6\%$, $n = 48$), alligators fed on experimental rations actually received more dry matter of food per feeding than did the controls. It is important to point out, however, that nutria fed in excess of the amount used here has been reported to result in gout (McNease and Joanen 1981; Coulson and Hernandez 1983); this condition was not a problem in the current study, despite the higher dry matter consumption by experimental diet treatment groups.

The amount fed was adjusted approximately every 2 to 3 weeks after body weights were taken, in order to maintain this feeding rate. For purposes of calculating the amount to be fed, the average weight of all "small" animals and of all "large" animals was used, across treatments. This undoubtedly slowed the growth of the faster growing treatment groups, somewhat, and therefore narrowed the differences in treatment effects. The weight of food offered and of food not consumed was also recorded at each feeding.

At the beginning of the experiment, alligators were fed mixtures of first 1:2 and then 2:1 of the moistened experimental diet:nutria, respectively for 4 feedings and 5 feedings, respectively. After these 17 days of feeding, alligators in the experimental treatment groups were completely weaned off of any nutria and were being fed solely the experimental diets.

Individual weights of each alligators were recorded at the beginning and end of the experiment. Weights of 6 selected individuals from each tank were recorded, as well as the total weight of all the animals in the tanks. The six largest alligators from each tank, among the largest in that tank, were chosen on the basis of their apparently successful acceptance of their experimental quarters and diet. The feeding trial lasted a total of 79 days. Weight data recorded over the period of the feeding trial was used to assess growth performance.

Results and Discussion

Weight-gain data for alligators maintained on the experimental diets and nutria are shown in Table 5. Analyses of variance indicated that growth responses differed significantly between diets ($F = 32.86$, $df = 15$, $p < 0.0001$, and $F = 2.87$, $df = 95$, $p < 0.001$, for tank average and individual weights, respectively. Results are generally similar, whether comparisons are made on the basis of the average weight for each tank or the average of all 6 individually recorded weights per tank. The basal diet was the most successful in that it produced growth not significantly different from that of the nutria-fed alligators for the six selected individuals in each tank. Diet 1-2 best approached that of the basal diet, but since it was not superior, there appeared to have been no advantage in adding lysine to the diet. Adding methionine depressed growth significantly in most cases, as did the additions of calcium and phosphorus (Diets 1-5 and 1-7). Addition of fat (poultry oil) to raise the energy levels similarly did not result in significantly improved growth.

Table 6 summarizes food consumption and conversion. On a wet weight basis, alligators ate a greater percentage of the nutria diet than the formulated rations. This may have resulted from difficulty in ingesting the formulated food, which was frequently walked-over and packed-down by the alligators which ate first. The next best-consumed diet (basal) was the experimental diet which supported best growth. Feed conversions for nutria meat were significantly better than those of the formulated rations. The latter were all similar in value, with the exception of those containing added calcium and phosphorus.

If we accept that equal growth can be maintained on either nutria or the basal diet, at the dry matter feeding levels used in this experiment, it would take approximately 2.7 (1.80/.66) times as much dry matter of formulated ration as that of nutria to achieve that equal growth. Since nutria carcasses, on a dry matter basis, are substantially more expensive than many commonly used animal by-product feedstuffs (Table 7), this 2.7:1 margin may not be a barrier to the farmer, who would benefit from the many advantages associated with a dry formulated feed. Nevertheless, to suggest that the basal diet be used as a basis to formulate a commercially viable feed for the alligator industry is highly premature. Many questions must be answered in order to "refine" formulated feeds for alligators and achieve satisfactory feed consumption, conversion, and growth responses. One such question is addressed in the next experiment.

II. THE EFFECTS OF DIETARY CALCIUM AND PHOSPHORUS ON THE GROWTH OF ALLIGATORS

Introduction

Results from Experiment I, as reported above, showed a growth depression resulting from the addition of calcium (Ca) and phosphorus (P) to the diets of alligators. However, the levels of these minerals in diets of that experiment were much higher than those used in feeds for other livestock species. Since many of the animal by-product feed ingredients considered to be of potential use in alligator feed formulation contain relatively large amounts of these minerals, it is essential to determine the response of alligators to a range of dietary calcium and phosphorus. The present experiment was initiated to (1) determine to what extent alligator growth, feed consumption, and/or feed utilization are affected by dietary calcium and phosphorus, (2) to indicate what levels of Ca and P are appropriate for alligator diets, and (3) to determine whether the optimal Ca:P ratio for alligators is 2:1, as for most animals.

Materials and Methods

Procedures used in this experiment were similar to those followed in Experiment I, with the following exceptions. Nine or ten animals were kept in each tank, and animals were no longer classified as large or small. Body weight variation was considerable (94 to 321g), but an attempt was made to ensure that the range of variation and the average body weight of alligators in each tank was similar (average = 193.0 g, ranging from 190.4-199.2 g). Animals from Experiment I were used. Each treatment group contained approximately the same number of animals from each of the treatment groups of Experiment I in order to equally distribute any residual effects from those previous treatments. During the course of the twelve week experiment, body weights of each animal were recorded at 4 week intervals. Average tank water temperatures ranged from 29.0° to 30.3°C, while minimum and maximum recorded temperatures were 25.4° and 33.2°C, respectively.

In this experiment, diets were mixed with water such that the dry feed comprised 50 to 58% of the food offered. Prior to initiating the experiment, all alligators were fed for approximately 6 weeks on a diet consisting of approximately 75% nutria meat and 25% extra lean beef fortified with vitamins. Most alligators used in the current experiment had eaten a moistened meal (in Experiment I) and it was possible to "wean" the alligators from the meat onto experimental diets after only four feedings. Alligators were

fed three times per week, and tanks were cleaned after each feeding. Water and air temperatures were similar to those in Experiment I.

Diets with a protein content and amino acid balance similar to that of the basal diet of Experiment I were formulated using ingredients with low levels of Ca and P (Table 8). Gelatin and carboxymethyl cellulose were each added at 2% of diet as a binder. A source of potassium (potassium carbonate) was added to raise the calculated level of potassium in the diet to 1%, since this was approximately the level found in nutria carcass (Table 2). A trace mineral premix, formulated for use in poultry rations, was also added to diets in this experiment, as opposed to Experiment I.

Rations were formulated so that Ca and P levels varied, as shown in Table 8. This was accomplished by adding different amounts of feed grade dicalcium phosphate (21% Ca, 18.5% P), deflourinated phosphate (32% Ca, 18% P), sodium phosphate (22% P), and limestone (38% Ca). Sand was used as a filler to maintain the isocaloric and isonitrogenous status of the diets. An alligator vitamin premix was again added at 1% of diet on a dry matter basis. Poultry oil was added to raise the ether extract to approximately 5%.

Results and Discussion

Data on food consumption, food conversion, mortality and growth are summarized in Tables 9 and 10. During the final four week period of the 12 week study, food consumption and growth decreased dramatically in all treatment groups. The causes for this are uncertain, but we believe they are not due to nutritional insufficiency, and that the general results described here are valid and useful in feed formulation. We believe data for the second month of the study to be most representative, as the animals' condition had not worsened by this time, and raw meat had been completely removed from the diet several weeks before.

Analyses of variance indicated differences among treatment mean weight gains for the total 12 week study ($F = 6.40$, $df = 11$, $p < 0.02$) as well as weeks 5-8 ($F = 8.01$, $df = 11$, $p < 0.01$). Alligators receiving Diet 2-1 (1% Ca, 0.5%P) grew significantly better than did those receiving other diets during weeks 5-8. Generally, growth decreased as the percentage of these minerals increased or as the ratio of Ca/P departed from 2:1.

During the first two months of the study, alligators ate between 64.9 and 92% of the food offered to them during any one month. There is no apparent relationship between diet and food conversion. Instead, diets which were consumed most tended to result in increased growth performance.

It is noteworthy that the feed conversion experienced during the initial two periods of this study was substantially better than that in the previous feeding trial (Experiment I). The reason for this improvement could have been the decreased Ca/P levels used in this diet, but the enhanced feed efficiency may also have been a result of the mineral modifications described above. The exact reason or reasons may be left for later research, but the results of this experiment have important implications for the development of a commercially viable formulated feed for the alligator industry. As noted previously, the basal diet of Experiment I, on a basis of feed cost/unit of body weight gain, bordered on economic viability. The feed efficiencies reported here represent an improvement of approximately 33% over those in Experiment I. Likewise, growth on Diet 2-1 was approximately 33% better than that of Diet 2-6, which is the diet of this experiment which most resembles that of the basal diet of Experiment I.

Hence, the nutrient profile of Diet 2-1 of this experiment is closer to that which might serve as a guide for an attempt at a commercially feasible ration. Nevertheless, it should be pointed out that nutria meat was converted to alligator body mass (in Experiment I) more efficiently than were diets in this experiment, again by a factor of about one-third.

Summary

This report discusses and researches some of the basic needs for making conventional feed formulation and manufacture a reality in the alligator industry. Although information about the nutrition of and manufacture of feed for other species may be useful, the unique nature of crocodilians creates a need for carefully planned research. Of primary importance is knowledge of the nutrient requirements of alligators as well as the ability of these reptiles to utilize nutrients in commercial feedstuffs. It would also be of great value to the alligator feed formulator, for a variety of reasons, to expand the list of feedstuffs now available for alligator rations.

An initial attempt was made at characterizing the nutrient profile of nutria meat and alligator eggs. This information provided guidelines for formulating a basal diet subsequently used in experiments to investigate the effects of various forms of nutrient supplementation.

In these feeding trials, a total of 13 formulated rations were used. Diets were formulated in order to allow comparison between treatments which would answer specific nutritional questions. It was found that these questions could be answered by examining growth data after about three months, and feeding trials were restricted to approximately that time period.

In the first feeding trial (Experiment I), a high protein diet was formulated with an amino acid balance derived from the amino acid composition of nutria, fish, alligator egg, and chicken egg protein. It was determined that adding lysine (2% of diet), methionine (1%), or both resulted in poorer growth performance. Adding calcium and phosphorus to a diet already high in these minerals resulted in poorer growth as well. Adding a source of fat (poultry oil) to diets did not result in significantly improved growth.

In the second feeding trial (Experiment 6), the effect of calcium and phosphorus on growth performance and feed conversion was studied further. A basal diet with an amino acid composition similar to the best-performing diet in Experiment I was formulated with feed ingredients low in calcium and phosphorus. Dietary levels of calcium and phosphorus were increased by adding various sources of these minerals. A total of six diets were formulated in this manner and were maintained isocaloric and isonitrogenous. Preliminary results indicate that the amounts of calcium and phosphorus in the diet did affect growth performance. Alligators fed a diet containing 1% calcium and 0.5% phosphorus grew best. Results also suggested that the ratio of Ca:P should be maintained at 2:1.

ACKNOWLEDGEMENTS

This work was supported by a grant from the Louisiana Department of Wildlife & Fisheries and a contract (DE-AC09-76-SR00819) between the Institute of Ecology at the University of Georgia and the United States Department of Energy. We are particularly indebted to Ted Joanen, Larry McNease and other personnel of the Rockefeller Wildlife Refuge for assistance and encouragement. The University of Georgia Research Foundation, Graduate School, Department of Poultry Science and Institute of Ecology kindly provided support in many forms.

Our work has been greatly enhanced by the assistance and interest of many individuals. We are indebted to Ted Joanen for helpful criticism of the manuscript and to R. A. Coulson for collaboration in laboratory studies. Allison Staton, Dan Kopp, Robert Fish, and Hardy Edwards, Jr., also provided invaluable assistance and support. We thank Jim Scharnagel of the Georgia Department of Natural Resources for issuance of permits required to perform this research. The manuscript was patiently and professionally typed by Janice Sand.

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Table 1. Nutrient profiles of some feedstuffs of potential use in feed formulation for alligators. Information summarized from Feedstuffs (1983, 1986) and NRC (1984).

| | Unit | Blood | Animal Fat | Fish Meal (Menhaden) | Fish Meal (AAFCO) | Meat Meal (Rendered) | Meat & Bone Meal (50%) | Crab Meal | Poultry By-Products Meal | Feather Meal |
|------------------------------|--------------------|------------|------------|----------------------|-------------------|----------------------|------------------------|-----------|--------------------------|--------------|
| General | | | | | | | | | | |
| Price | \$/lb | 0.165 | 0.10 | 0.148 | - | - | 0.92 | - | 0.11 | 0.58 |
| Dry Matter | % | 89.3-93.0 | 99.5 | 92 | 88.4 | 92-92.8 | 92.6-93 | 95.0 | 93-94 | 93 |
| Crude protein | % | 80.0-88.9 | 0.0 | 60.5-62.0 | 59.0 | 54.4-55 | 50-50.4 | 30.0 | 58 | 86.4 |
| Crude fiber | % | 0.6-1.0 | - | 0.7-1.0 | 1.0 | 2.5-8.7 | 2.8 | 10.5 | 2-2.5 | 1 |
| Crude fat | % | 1.0 | 99.4 | 9.4-10.2 | 5.6 | 7.1-7.2 | 8.5-8.6 | 2.2 | 13-14 | 3.3 |
| Ash | % | 4.4 | - | 20.0 | 20.2 | 33.0 | 33.0 | 31.0 | 16.0 | - |
| Linoleic Acid | % | 0.1 | - | 0.12 | - | 0.28 | 0.036 | - | 2.54 | - |
| Minerals | | | | | | | | | | |
| Calcium | % | 0.06-0.28 | - | 5.0-5.11 | 5.5 | 7.6-8.27 | 9.2-10.3 | 18.0 | 3-4.0 | 0.33 |
| Phosphorus | % | 0.09-0.42 | - | 2.88-3.0 | 3.3 | 4.0-4.1 | 4.7-5.1 | 1.5 | 1.7-2.4 | 0.55 |
| Potassium | % | 0.41-0.90 | - | 0.72-0.77 | 0.39 | 0.55-0.60 | 1.02-1.4 | 0.45 | 0.3-0.6 | 0.31 |
| Sodium | % | 0.31-0.33 | - | 0.34-0.41 | 1.07 | 1.15-1.6 | 0.72-0.73 | 0.85 | 0.40-0.28 | 0.71 |
| Magnesium | % | 0.22-0.40 | - | 0.14-0.16 | 0.21 | 0.27-0.58 | 1.12-1.13 | 0.88 | 0.22-0.15 | 0.20 |
| Sulfur | % | 0.32 | - | 0.45 | 0.24 | 0.49-0.5 | 0.26-0.5 | 0.04 | 0.51 | 1.50 |
| Manganese | mg/kg | 5.3-6.0 | - | 33-35.6 | 22.8 | 9.5-10 | 12.3-14 | 133.0 | 11 | 21 |
| Iron | mg/kg | 380-3000 | - | 438-440 | 360 | 440 | 490-500 | 440 | 440 | 76 |
| Copper | mg/kg | 3-9.9 | - | 11-11.4 | 14.6 | 9.7-10 | 1.5-2 | 32.8 | 14 | 7 |
| Zinc | mg/kg | 306 | - | 147-151 | n.a. | 103 | 93 | 102 | 120 | 54 |
| Selenium | mg/kg | - | - | 2.10-2.2 | 1.5-2.0 | 0.4-0.42 | 0.25 | 3.8 | 0.5-1.0 | 0.84 |
| Vitamins | | | | | | | | | | |
| Carotene | mg/kg | - | - | - | - | - | - | - | - | - |
| Vitamin A | 10 ⁶ /g | - | - | - | - | - | - | - | - | - |
| Vitamin E | mg/kg | - | 7.9 | 5.7-7 | 18.5 | 1 | 0.8-1.0 | - | 2-2.2 | - |
| Thiamin (B ₁) | mg/kg | 0.44-0.5 | - | 0.2-0.5 | 1.3 | 0.2 | 0.2-0.8 | - | 1 | 0.1 |
| Riboflavin (B ₂) | mg/kg | 1.3-1.5 | - | 4.8-4.9 | 6.5 | 5.2-5.5 | 4.4-5.2 | 7.5 | 10.0-11 | 2.1 |
| Pantothenic Acid | mg/kg | 1.1-5.0 | - | 8.8-9 | 8.7 | 5-5.8 | 4.1-4.4 | 6.6 | 8.8-12.3 | 10 |
| Biotin | mg/kg | 0.08-0.2 | - | 0.15-0.20 | n.a. | 0.14-0.17 | 0.14-0.64 | n.a. | 0.30 | 0.44 |
| Folic Acid | mg/kg | 0.08-0.4 | - | 0.6-1 | n.a. | 0.3-0.6 | 0.3-0.6 | n.a. | 1 | 0.2 |
| Choline | mg/kg | 280-990 | - | 3056-3080 | 3510 | 2007-2200 | 1996-2000 | 2024 | 5952-5980 | 891 |
| Vitamin B ₁₂ | mg/kg | 44 | - | 104-150 | 250 | 68-90 | 70-100 | 448 | 310 | 78 |
| Niacin | mg/kg | 13-31.0 | - | 55 | 60.8 | 57-59.4 | 46-59.4 | 44.0 | 39.6-40 | 27 |
| Pyridoxine (B ₆) | 4.4 | - | 4 | - | 3 | 12.8 | - | 414 | 3.0 | - |
| Amino Acids | | | | | | | | | | |
| Arginine | % | 2.35-3.81 | - | 3.23-3.79 | 3.73 | 3.7-3.73 | 3.35-3.62 | 1.7 | 3.84-4 | 5.42 |
| Glycine | % | 4.0-4.4 | - | 3.88-4.19 | 3.93 | 6.30 | 6.79-6.9 | 1.8 | 2.93-5.90 | 6.31 |
| Serine | % | 3.86 | - | 2.25 | - | 1.60 | 1.88 | - | 3.68 | 9.26 |
| Histidine | % | 3.05-5.26 | - | 1.44-1.46 | 1.53 | 1.1-1.30 | 0.90-0.96 | 0.5 | 1.50-1.61 | 0.34 |
| Isoleucine | % | 0.8-0.88 | - | 2.83-2.85 | 3.64 | 1.60-1.9 | 1.40-1.7 | 1.2 | 2-2.33 | 3.26 |
| Leucine | % | 10.3-11.82 | - | 4.5-5.0 | 4.69 | 3.32-3.5 | 2.80-3.2 | 1.6 | 3.70-4.4 | 6.72 |
| Lysine | % | 5.3-8.85 | - | 4.7-4.83 | 5.17 | 3.00 | 2.60 | 1.4 | 2.57-2.70 | 1.67 |
| Methionine | % | 0.75-1.0 | - | 1.78-1.8 | 1.72 | 0.75 | 0.65-0.67 | 0.5 | 1-1.04 | 0.42 |
| Oxystine | % | 0.86-1.4 | - | 0.56-0.6 | 0.57 | 0.66-0.68 | 0.25-0.33 | 0.2 | 0.69-1.0 | 4 |
| Phenylalanine | % | 5.1-6.55 | - | 2.28-2.48 | 0.67 | 1.70-1.9 | 1.50-1.7 | 1.2 | 1.79-2.10 | 3.26 |
| Tryptophan | % | 1.0-1.34 | - | 0.72-0.68 | 2.68 | 0.35-0.36 | 0.26-0.28 | 0.3 | 0.53-0.55 | 0.50 |
| Threonine | % | 3.8-3.94 | - | 2.34-2.50 | 2.49 | 1.74-1.8 | 1.50-1.63 | 1.2 | 2-2.03 | 3.43 |
| Valine | % | 5.2-8.60 | - | 3.23-3.43 | 3.26 | 2.30-2.6 | 2-2.25 | 1.5 | 2.60-2.65 | 5.57 |

Table 2. Analyses of nutria carcass (excluding pelt and viscera) and homogenates of whole alligator eggs, excluding shells. Samples of nutria (n=20) and alligator egg (n=4) homogenates were pooled and analyzed in duplicate.

| Nutrient | Nutria | Alligator Egg |
|-------------------|--------|-----------------|
| General | | |
| Ash (5) | 19.03 | 5.44 |
| Ether Extract (%) | 8.46 | 40.80 |
| Total Lipids (%) | 10.44 | 49.14 |
| Crude Protein (%) | 70.57 | 42.51 |
| Crude Fiber (%) | 0.18 | 0.063 |
| Minerals | | |
| Calcium (%) | 6.03 | NA ¹ |
| Phosphorus(%) | 3.40 | NA |
| Sodium (%) | 0.33 | NA |
| Potassium (%) | 1.03 | NA |
| Chlorine (%) | 0.32 | NA |

¹ Analysis not available.

Table 3. Partial amino acid analyses of protein in nutria, fish, alligator egg, chicken egg, and the basal diet of Experiment (I).

| Amino Acid | % of Protein in: | | | | |
|---------------|---------------------|-------------------|----------------------------|--------------------------|-------------------------|
| | Nutria ¹ | Fish ² | Alligator Egg ¹ | Chicken Egg ³ | Basal Diet ⁴ |
| Arginine | 5.74 | 3.42 | 5.91 | 6.40 | 5.3 |
| Glycine | 17.44 | 7.08 | 9.92 | 3.24 | 6.1 |
| Serine | 5.10 | 5.70 | 9.62 | 7.60 | 5.7 |
| Histidine | 3.53 | 2.61 | 4.48 | 2.32 | 3.4 |
| Isoleucine | 3.06 | 5.18 | 5.14 | 4.98 | 3.3 |
| Leucine | 8.53 | 7.13 | 9.27 | 8.30 | 9.7 |
| Lysine | 9.42 | 8.32 | 11.00 | 7.07 | 7.5 |
| Methionine | NA ⁵ | 0.38 | NA | 3.24 | 1.7 |
| Cystine | NA | 0.38 | NA | 2.20 | 1.2 |
| Phenylalanine | 3.41 | 4.18 | 2.93 | 4.70 | 5.3 |
| Tyrosine | 2.00 | 6.51 | 1.75 | 4.40 | 3.9 |
| Threonine | 4.60 | 3.75 | 7.11 | 4.98 | 4.2 |
| Tryptophan | NA | 1.81 | NA | 1.44 | 1.1 |
| Valine | 3.74 | 5.13 | 4.43 | 6.47 | 7.1 |

¹ By analysis (hydrolysis in 6N HCl 22 hrs 100° in vacuo).

² From Coulson and Hernandez (1983).

³ From Nesheim, Austic, and Card (1979).

⁴ By calculation.

⁵ Analyses not available.

Table 4. Experiment I: Experimental and control diets--% composition and calculated analysis.

| Ingredients | Diet | | | | | | | |
|-----------------------------|----------------|------|------|------|------|------|------|------------------|
| | 1-1 (Basal) | 1-2 | 1-3 | 1-4 | 1-5 | 1-6 | 1-7 | 1-8 ¹ |
| Casein | 20.0 | 19.6 | 19.8 | 19.4 | 18.6 | 18.8 | 18.1 | - |
| Blood meal | 25.0 | 24.5 | 24.8 | 24.3 | 23.3 | 23.5 | 22.6 | - |
| Fish meal | 15.0 | 14.7 | 14.9 | 14.6 | 14.0 | 14.1 | 13.5 | - |
| Feather meal | 10.0 | 9.8 | 9.9 | 9.7 | 9.3 | 9.4 | 9.0 | - |
| Meat & Bone meal | 17.0 | 16.7 | 16.8 | 16.5 | 15.8 | 16.0 | 15.3 | - |
| Poultry BP meal | 10.0 | 9.8 | 9.9 | 9.7 | 9.3 | 9.4 | 9.0 | - |
| Carboxymethyl Cellulose | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | - |
| Vitamin | 1.0 | 1.0 | 1.0 | 1.0 | 0.9 | 0.9 | 0.9 | 1.0 |
| NaCl | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | - |
| Lysine, 80% | - | 2.0 | - | 2.0 | 1.9 | 1.9 | 1.8 | - |
| DL Methionine | - | - | 1.0 | 1.0 | 0.9 | 0.9 | 0.9 | - |
| Ground Limestone | - | - | - | - | 1.4 | - | 1.4 | - |
| Phosphate, DiCal | - | - | - | - | 2.8 | - | 2.8 | - |
| Poultry Oil | - | - | - | - | - | 3.0 | 3.0 | - |
| Calculated Analysis | | | | | | | | |
| Moisture (%) ² | 6.9 | 6.8 | 6.9 | 6.8 | 6.6 | 6.6 | 6.4 | 74.0 |
| Protein (%) | 71.8 | 71.9 | 72.0 | 72.1 | 69.1 | 70.0 | 67.1 | 69.9 |
| Ether Extract (%) | 4.9 | 4.8 | 4.9 | 4.8 | 4.6 | 7.6 | 7.4 | 8.5 |
| Crude Fiber (%) | 1.1 | 1.1 | 1.1 | 1.0 | 1.0 | 1.0 | 1.0 | 0.2 |
| Calcium (%) | 3.0 | 2.9 | 3.0 | 2.9 | 3.9 | 2.8 | 3.8 | 6.0 |
| Available Phosphorus (%) | 1.8 | 1.7 | 1.7 | 1.7 | 2.1 | 1.6 | 2.1 | 3.4 |
| Potassium (%) | 0.5 | 0.5 | 0.5 | 0.4 | 0.4 | 0.4 | 0.4 | 1.0 |
| Chloride (%) | 0.7 | 0.7 | 0.7 | 0.7 | 0.6 | 0.6 | 0.6 | 0.3 |
| Lysine (%) | 5.4 | 6.9 | 5.4 | 6.8 | 6.5 | 6.6 | 6.3 | 6.6 |
| Methionine (%) | 1.2 | 1.2 | 2.2 | 2.2 | 2.1 | 2.1 | 2.0 | n/a |
| Cystine (%) | 0.9 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | 0.8 | n/a |

¹ Nutritional content by analysis; Control Diet (Ground Nutria Meat + Vitamins).

² Fed on a wet weight basis as a 50:50 mix with water; % moisture for diets 1-7 on a wet weight, as fed, was approximately 53.4%.

Table 5. Growth responses (g) to dietary treatment as compared by Duncan's multiple range test. Means with the same superscript are not significantly different.

| Diet | Treatment | Tank Average | Average of 6 Individuals |
|------|--------------------------|---------------------|-----------------------------|
| 1-8 | Nutria | 105.5 ¹ | 128.5 ^{1,2} |
| 1-1 | Basal | 96.2 ² | 131.9 ¹ |
| 1-2 | Basal + Lysine (Lys) | 94.1 ^{2,3} | 124.2 ^{1,2} |
| 1-3 | Basal + Methionine (Met) | 83.6 ⁴ | 98.3 ^{3,4} |
| 1-4 | Basal + Lys, Met | 85.5 ^{3,4} | 99.7 ^{3,4} |
| 1-5 | Diet 1-4 + Ca, P | 69.6 ⁵ | 88.4 ⁴ |
| 1-6 | Diet 1-4 + Fat | 83.0 ⁴ | 104.6 ^{2,3,4} |
| 1-7 | Diet 1-4 + Ca, P, Fat | 60.7 ⁵ | 79.1 ⁴ |

Table 6. Consumption and food conversion (tank totals) for the "post-weaning" period (days 17-79).

| Diet | Treatment | Consumption (g/wk/animal) | | Food Conversion ¹ | |
|------|--------------------------|---------------------------|--------|------------------------------|--------|
| | | Wet Wt | Dry Wt | Wet Wt | Dry Wt |
| 1-1 | Basal | 28.2 | 13.1 | 3.17 | 1.82 |
| 1-2 | Basal + Lysine (Lys) | 25.3 | 11.8 | 3.00 | 1.72 |
| 1-3 | Basal + Methionine (Met) | 24.0 | 11.1 | 3.17 | 1.82 |
| 1-4 | Basal + Lys, Met | 24.2 | 11.3 | 3.24 | 1.86 |
| 1-5 | Diet 1-4 + Ca, P | 25.1 | 11.7 | 4.40 | 2.52 |
| 1-6 | Diet 1-4 + Fat | 25.3 | 11.8 | 3.62 | 2.07 |
| 1-7 | Diet 1-4 + Ca, P, Fat | 23.2 | 10.8 | 5.23 | 3.00 |
| 1-8 | Nutria | 29.1 | 7.6 | 2.75 | 0.66 |

¹ g food intake/g body weight gain on wet weight and dry weight basis of feed; body weight in wet weight only.

Table 7. Prices of commonly used animal by-product feed ingredients and commercially available ground nutria meat.

| Ingredient | \$/pound | |
|---------------------------------|------------|------------|
| | Wet Weight | Dry Weight |
| Nutria -- High ¹ | 0.16 | 0.53 |
| Nutria -- Low ¹ | 0.10 | 0.33 |
| Blood Meal ² | 0.162 | 0.185 |
| Feather Meal ² | 0.063 | 0.067 |
| Fish Meal ² | 0.153 | 0.166 |
| Meat and Bone Meal ² | 0.090 | 0.097 |
| Poultry BP Meal ² | 0.100 | 0.108 |

¹ Assumes 30% dry matter.

² Atlanta prices, Feedstuffs, January 27, 1986.

Table 8. Experiment II: Composition of experimental diets.

| | Diet | | | | | |
|---------------------------------------|------|------|-------|------|------|------|
| | 2-1 | 2-2 | 2-3 | 2-4 | 2-5 | 2-6 |
| <u>Ingredients (% of Diet)</u> | | | | | | |
| Casein | 36.6 | 36.6 | 36.6 | 36.6 | 36.6 | 36.6 |
| Blood meal | 27.7 | 27.7 | 27.7 | 27.7 | 27.7 | 27.7 |
| Feather meal | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 |
| Poultry oil | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 |
| Gelatin | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 |
| Vitamin premix | 1.0 | 1.0 | 1.0 | 1.0 | 1.0 | 1.0 |
| Salt | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 |
| Chromic Oxide | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 |
| Potassium carbonate | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Trace mineral premix ¹ | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| L-Arginine | 0.2 | 0.2 | 0.2 | 0.2 | 0.1 | 0.1 |
| dL-Methionine | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Dicalcium phosphate | - | - | - | 3.8 | - | - |
| Sodium phosphate | - | - | 0.5 | - | - | - |
| Defluorinated phosphate | - | 2.0 | 5.3 | - | - | 7.8 |
| Limestone | 2.6 | 2.8 | - | 4.2 | 10.0 | 3.4 |
| Sand | 8.8 | 6.6 | 5.5 | 3.3 | 1.3 | 0.1 |
| <u>Nutrients</u> | | | | | | |
| Calcium (% of diet) | 1.00 | 1.50 | 1.50 | 2.00 | 3.00 | 3.00 |
| Phosphorus (% of diet) | 0.50 | 0.75 | 1.25 | 1.00 | 0.50 | 1.50 |
| Calcium : Phosphorus ratio | 2:1 | 2:1 | 1.2:1 | 2:1 | 6:1 | 2:1 |

¹ Trace mineral premix provides (in mg/kg diet): MnO₂, 222; ZnO, 150; FeSO₄·7H₂O, 200; FeCO₃, 83; CuSO₄, 29; Ca (IO₃)₂, 15.

Table 9. Percent food consumption, food conversion and mortality in alligators offered different dietary treatments over a 12-week period.

| Diet | Treatment | | % Food Consumed | | | g Dry Matter Consumed g Body Wt Gained | | | Mortality |
|------|-----------|------|-----------------|-------|-------|---|-------|-------|-----------|
| | % CA | % P | Weeks | Weeks | Weeks | Weeks | Weeks | Weeks | |
| | | | 1-4 | 5-8 | 9-12 | 1-4 | 5-8 | 9-12 | |
| 2-1 | 1.0 | 0.50 | 92.0 | 83.1 | 48.5 | 0.74 | 0.92 | 2.03 | 0 |
| 2-2 | 1.5 | 0.75 | 88.0 | 77.4 | 51.2 | 0.72 | 1.10 | 1.59 | 0 |
| 2-3 | 1.5 | 1.25 | 69.8 | 71.1 | 50.1 | 0.72 | 1.01 | 2.54 | 1 |
| 2-4 | 2.0 | 1.0 | 86.1 | 77.2 | 52.5 | 0.70 | 1.00 | 1.86 | 1 |
| 2-5 | 3.0 | 0.5 | 73.5 | 67.9 | 44.6 | 0.76 | 0.96 | 2.86 | 1 |
| 2-6 | 3.0 | 1.5 | 69.0 | 72.3 | 47.0 | 0.70 | 1.08 | 1.75 | 0 |

Table 10. Average body weight changes in alligators offered dietary levels of calcium and phosphorus over a 12-week period, as compared by Duncan's multiple range test. Values sharing the same superscript are not significantly different.

| Diet | Treatment | | Average Body Weight Gain (g) | |
|------|-----------|------|------------------------------|--------------------|
| | % Ca | % P | Weeks 1-12 | Weeks 5-8 |
| 2-1 | 1.0 | 0.50 | 221.3 ¹ | 100.0 ¹ |
| 2-2 | 1.5 | 0.75 | 210.9 ^{1,2} | 77.6 ² |
| 2-3 | 1.5 | 1.25 | 183.1 ^{2,3} | 80.9 ² |
| 2-4 | 2.0 | 1.0 | 214.1 ^{1,2} | 86.6 ² |
| 2-5 | 3.0 | 0.5 | 163.3 ³ | 74.4 ² |
| 2-6 | 3.0 | 1.5 | 182.2 ^{2,3} | 76.1 ² |

GEORGIA'S COASTAL ISLAND ALLIGATORS, VARIATIONS IN HABITAT AND PREY AVAILABILITY

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ABSTRACT - A protected coastal alligator population on a Georgia barrier island was studied by capture, tagging and recapture methods to determine the movement patterns of different size alligators. Prey availability was determined to be a criteria for movement to and from fresh, brackish and salt water habitats. Water level fluctuations were evident in all habitats. Alligator density was highest in freshwater ponds during winter denning and basking seasons. Brackish areas were exploited by alligators 1 to 2 m in total body length and tidal salt marshes were used by alligators more than 1.5 m total body length.

INTRODUCTION

The Georgia coastal zone has seen a dramatic human population increase in the last fifteen years. Understanding the habitat uses and environmental pressures placed on existing American alligator (*Alligator mississippiensis*) populations could help government planners and private developers from destroying the animals natural habitat and rangewide corridors. In coastal areas of Louisiana, Joanen and McNease (1972a) reported that 40.3% of the estimated alligator population could be found in fresh marsh habitat, 30.2% in intermediate marsh habitat, and 28.5% in brackish marsh habitat. American alligator movements have been described through tagging and radio telemetric studies in Florida (Goodwin and Marion 1979), Louisiana (Joanen and McNease 1970, 1972b), and Texas (Smith 1980). However, little was known of alligator movements and habitat preference within the coastal zone areas of Georgia. From 1975 the American alligator of Georgia's Atlantic coastal area has been the focus of studies sponsored in part by the Atlanta Zoological Society and the Department of Herpetology, Zoo Atlanta. This long term study concentrated on the subadult alligator population endemic to Wassaw Island. Additional observations and data were collected from Savannah River National Wildlife Refuge; Oatland, Skidaway, Ossabaw, Blackbeard, Little St. Simon's and Cumberland Islands. I here report data related to Georgia's coastal island American alligator population dynamics, rangewide movements, prey availability and environmental pressures.

STUDY AREA

The principle data collected during the study period from 1 June 1975 to 1 October 1986 came from Wassaw Island National Wildlife Refuge's American alligator population endemic to the 1,012 high ground ha of Great Wassaw Island (Fig. 1) and its surrounding estuary bordered by Odingsell River, Wassaw Creek, New Cut to Salt Pond Shoals, and Wassaw Sound. Wassaw Island was formed from a typical sand sharing development of dune ridges beginning during the Holocene Period. Still under the same wind and wave action today, the island is slowly changing as the beachfront erodes from the north end and exposes the forests in that area to a pounding surf whose powerful currents shift and deposits sands on the south end of the island where emergent plants and forests rebuild the ecosystem. Great Wassaw Island consists mainly of a virgin forest of live oak, slash pine, mixed hardwoods and beach dune communities in

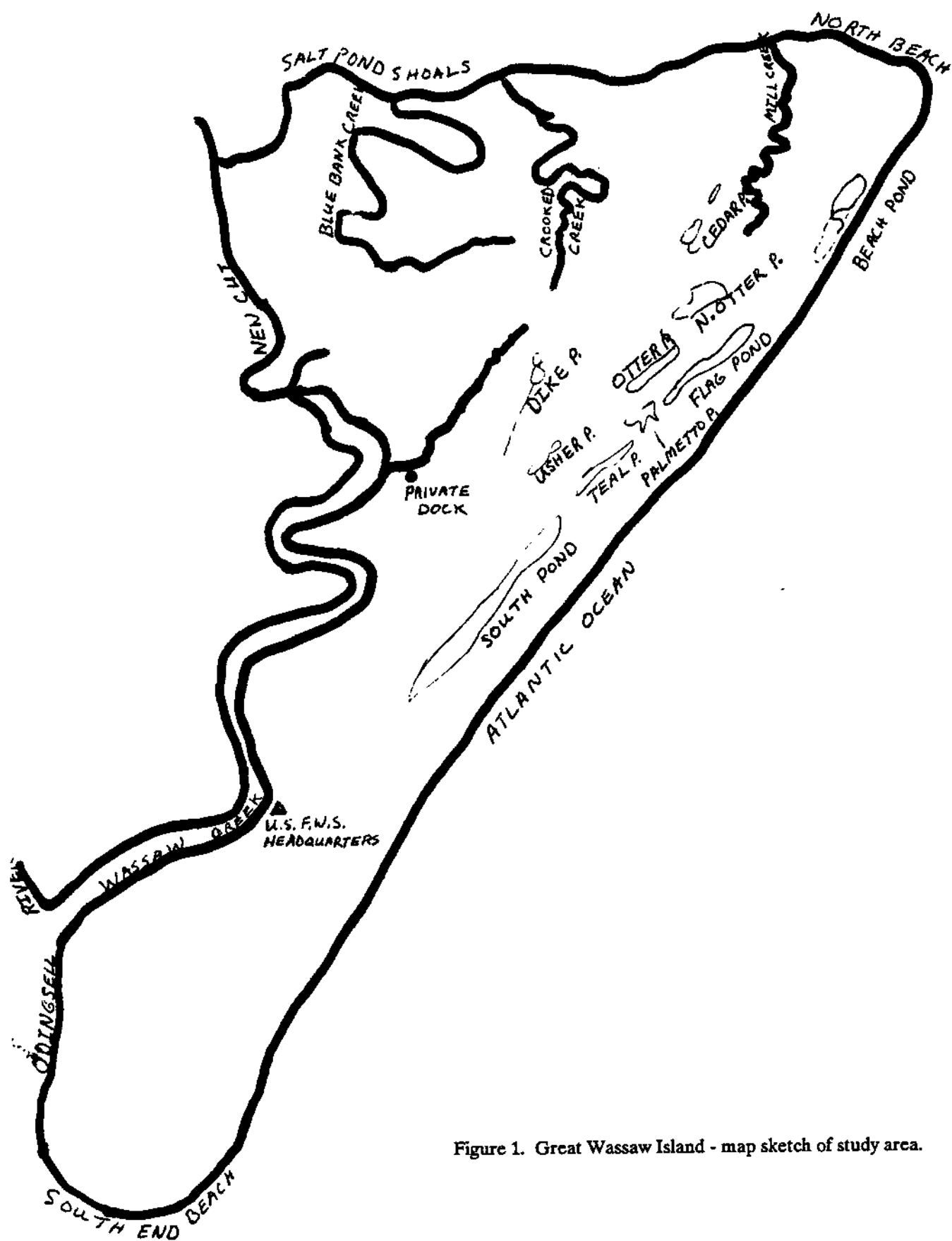


Figure 1. Great Wassaw Island - map sketch of study area.

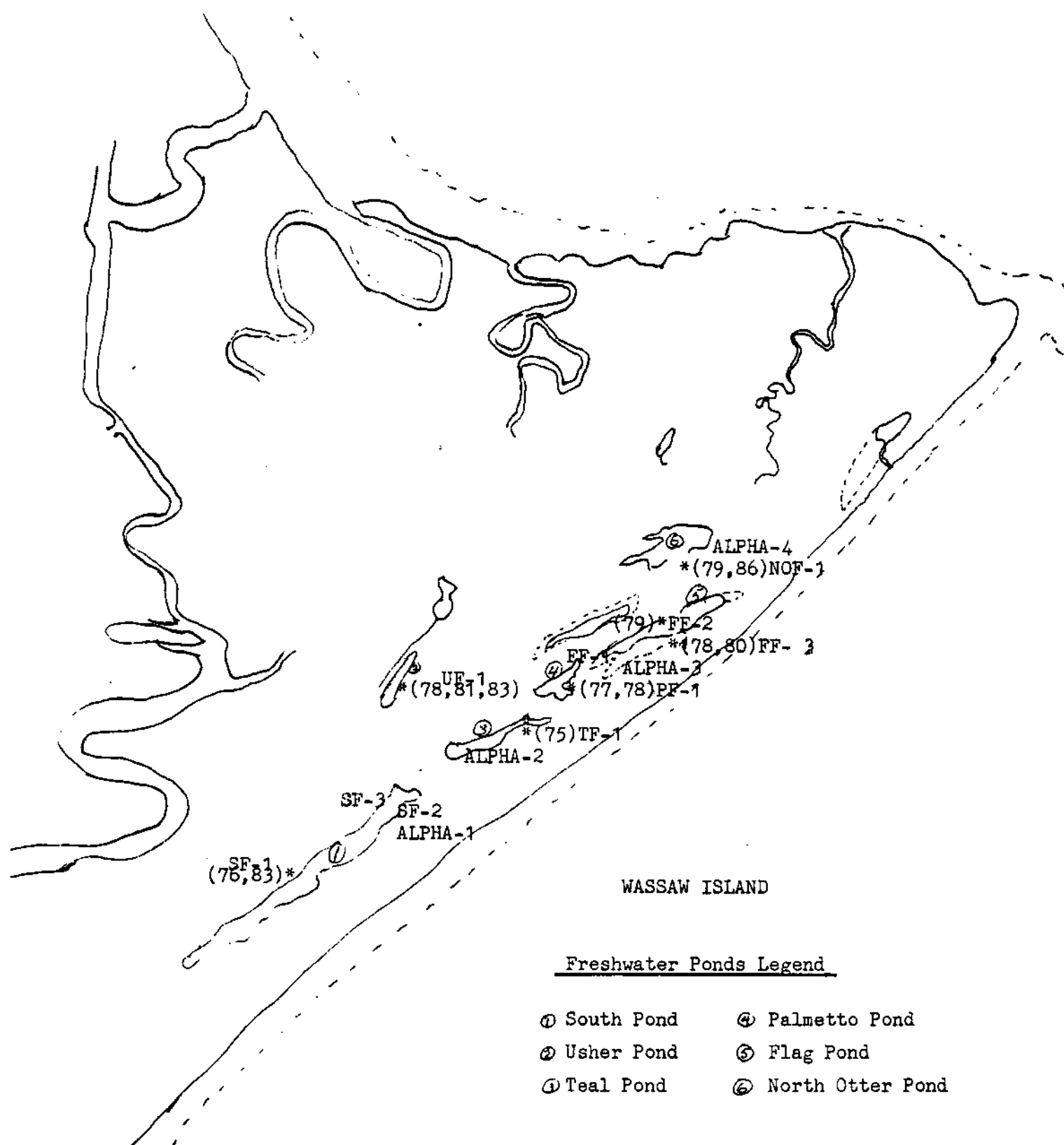


Figure 2. Distribution of known adult breeding American alligators on Wassaw Island.

various stages of development. Interior ponds were formed as swales and sloughs were isolated by new beach front dune ridges. Some ponds retain feeder creeks to the tidal marshes allowing for excess drainage of rainwater and incoming salt water on spring tides associated with full and new moons. These shallow brackish ponds remain relatively clear of vegetation and do not fluctuate as rapidly as the freshwater ponds or tidal creeks and serve as a seasonal nursery area for striped mullet, tarpon, shrimp and blue crabs. The brackish ponds are Cedar Pond, fed and drained by the Cedar Creek branch of Mill Creek; Otter Pond, fed and drained by Mill Creek; Dike Pond, fed and drained by Crooked Creek; and Beach Pond, which has undergone several changes since 1970. Beach Pond was an isolated interior freshwater pond fed by rainfall, but during a storm in the winter of 1970, the beach dune was eroded and salt water intrusion began forming a channel for daily tidal influx. This condition remained until 1982 when another dune ridge formed and isolated the twelve year old estuary forming a brackish pond with intermittent levels of rainwater and occasional spring tides cresting the dune ridge.

Beach Pond is basically a shallow pan and susceptible to drought conditions, mud cracking, and browning of vegetation. The rainfed freshwater ponds are the nesting and nursery areas of the adult females and their hatchlings (Fig. 2). The largest, the 18.2 ha Flag Pond, is vegetatively choked with < 3.5 m high cattails, wild hibiscus and needle grass. Guarded from the sea by a 10 m high dune ridge, Flag Pond is tunneled with gator trails and dotted with dens. Bordering meadows and willow trees are used by deer and by herons and egrets as nesting areas. North Otter Pond, Teal, Palmetto, Usher and South Ponds are the remaining freshwater habitats. Because freshwater ponds are subject to occasional drought conditions, no large freshwater fish species exist on Wassaw Island. The salt marsh estuary surrounding Great Wassaw Island is nearly 75% of the total refuge system. Flooded and drained twice daily, the marshes are subject to mean tidal change of 2.3 m and spring tides range > 3 m several times a year.

For the purposes of this study, alligators were located primarily at night using 12 volt head and hand held lamps and captured by hand or with wire-noose poles. Once captured, each alligator was tagged in the webbing between digits with a Number 1 size National Band and Tag Co. 1005 monel steel stamped tag (Fig. 3) and a numerical code was punched through the last four rows of double dorsal caudal scutes and the first eight single dorsal caudal scutes (Fig. 4) using a coding method described by Bustard and Choudhury (1981). Larger alligators had Hasco Company metal tags affixed to the first single caudal scute. For identification by observation, three or more colored rings were placed through the punched holes and when read from anterior to posterior the colored rings indicated the ranking capture of a certain alligator in a designated habitat of a particular year.

The following data were recorded from each capture:

- Head Length (HL) - straight line distance between premaxilla and supraoccipital points
- Head Width (HW) - straight line distance between quadratojugal points
- Total Body Length (TBL) - straight line distance - premaxilla to tail tip
- Body Girth (BG) - circumference of body posterior to front limbs
- Tail Length (TL) - straight line distance from vent posterior to tip of tail
- Body Temperature (BT) - cloaca reading
- Air Temperature (AT) - ambient
- Water Temperature (WT) - pond, pool, creek, etc.
- Ground Temperature (GT) - surface temperature
- Habitat Locality (HL) - e.g. pondsite
- Time of Capture (time) - 24 hour system

A printed data sheet was developed for field use (Fig. 5).

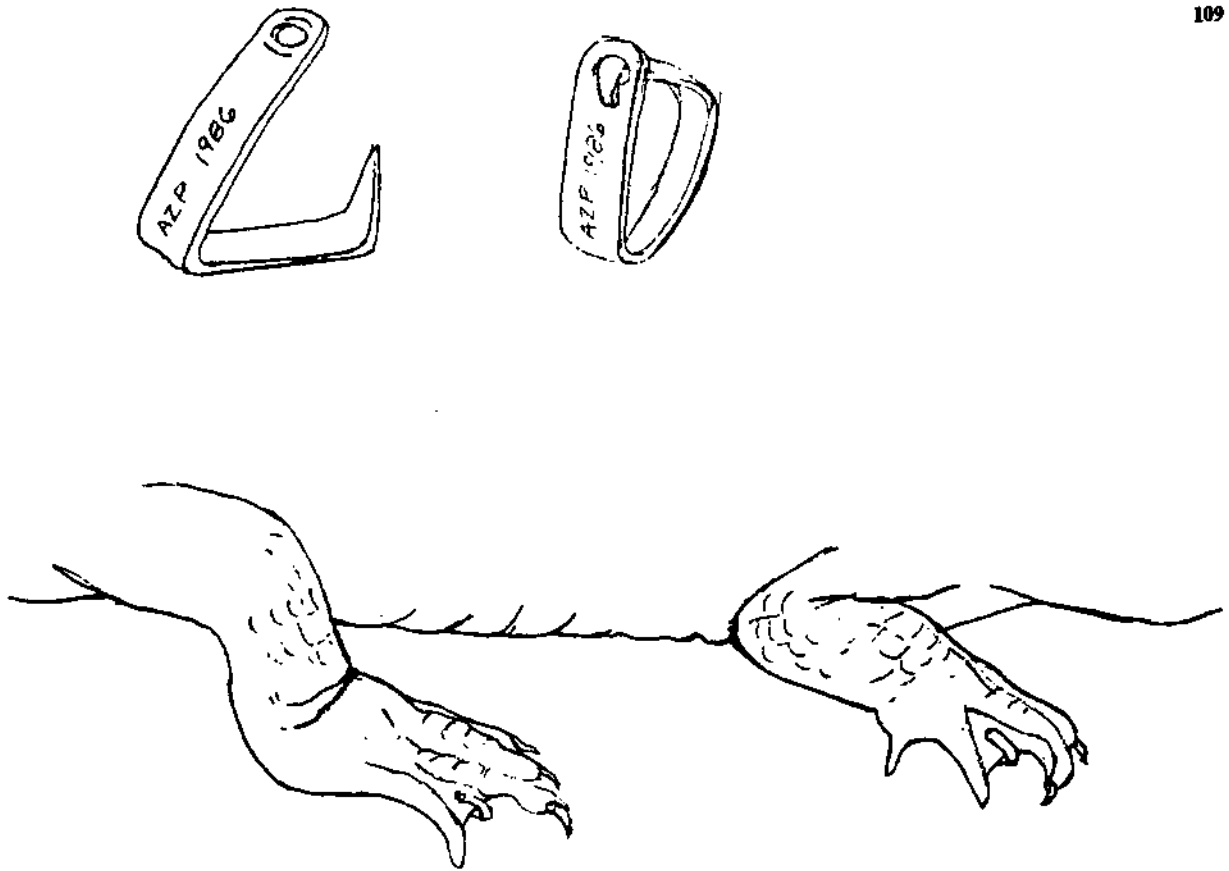


Figure 3. Example of metal tags applied to webbing between digits.

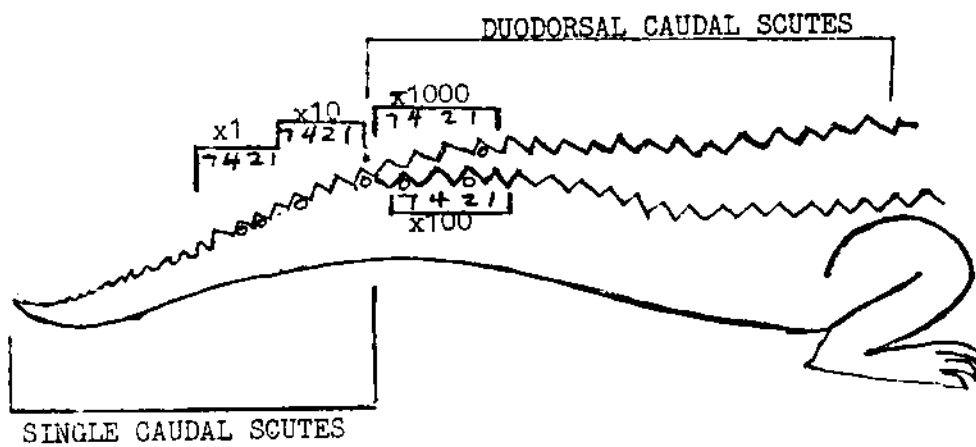


Figure 4. Punch coding and marking technique using the posterior four duodorsal caudal scutes and the anterior eight single caudal scutes (e.g. the scutes with punched holes indicate the number 1986).

D 82-1

American Alligator
Field Data Sheet

Date June 15, 1982 Time 1:30
 Capture Site Dike Pond - Brickish
 Quadrant _____
 Captured by Tamarack, Simon, Howard
 Assistant(s) Boam, Howard
 Method of Capture _____
 Hand(s) _____ Pole ☒
 Net _____ Other _____
 Remarks _____

Temperatures

Body(internal) 29°C Air 32°C
 Water 29°C Ground _____

Measurements 127.8 cm.

Total Body Length 49.2 inches
 Body Girth 39.9 cm
 Tail Length 25 inches 64.2 cm.
 Tail Girth 27.5 cm
 Head Length 17.5 cm
 Head Width 8.75 cm
 Body condition and abnormalities
none

Identification Record

Sex M

Tagging Information

| | old tags | new tags |
|-----------------|-------------------------|----------------|
| Toe Tag | <u>443 RF</u> | <u>-445 RR</u> |
| Caudal tag | _____ | _____ |
| Caudal Punch | <u>343</u> | _____ |
| Ring Color Code | <u>White-Black-Blue</u> | |

Additional information

Signed and Recorded by :
BERRY SEAN

Figure 5. Copy of field data sheet.

Each alligator captured was given a file code identification and plotted on an aerial photo map to monitor and chart movement patterns. The file code was identical to the ring color code system used in the caudal scutes. The habitat (Designated Letter Abbreviation), year of capture, ranking order of capture, for example:

F80-3 - 3rd individual captured in Flag Pond in 1980
 MC78-1 - 1st individual captured in Mill Creek in 1978
 NO86-10 - 10th individual captured in North Otter Pond in 1986.

Alligators were classified by size using the following formula:

| <u>Size TBL</u> | <u>Classification</u> |
|-------------------------------------|-----------------------|
| Hatchlings | Neonate |
| .5 m - 1 m | Juvenile |
| 1 m - 2.5 m | Subadult |
| Adult breeding size female (> 2 m) | Alpha female |
| Subdominate male (2.5 - 3 m) | Beta Male |
| Dominate male breeder (> 3 m) | Alpha Male |

RESULTS

Population Dynamics - From observations made in 1975 and 1976, a population estimate (including neonates) of 250 plus or minus 50 individual *A. mississippiensis* was made. The breeder adults were not deliberately disturbed by attempted capture and only two Alpha females were captured when they had vacated their territorial limits. Four Alpha males are credited with the courtship and mating of the ten known breeding and nesting Alpha female adults. Three Beta males, sexually mature but physically undersized, were captured and often showed wounds which could have been the results of fighting and territorial aggression. Beta males were not observed in the fresh water ponds after mid May, the courtship time table, and remained in the tidal marshes until the fall denning season.

The largest segment of the population consisted of subadult females and males, juveniles and neonates. Nests and neonates were never guarded from humans by the females on Wassaw Island. However, known nesting was successful 70% of the time and hatching rates were average or above other study areas. Predation and loss of hatchlings because of winter kill and drought were the greatest influences in population dynamics. As would be expected, years of high nesting density and successful hatching pushed the estimated island alligator population to 300+ individuals, and when nesting and successful hatchling survival were low the population estimate was dropped to 200 individuals (Fig. 6).

Population Dispersion - The 1976 and 1977 observation surveys of the early spring emerging Wassaw Island alligators from their winter dens established that the resident population (over winters) in the six freshwater ponds often denned communally with breeder females and their offspring including neonates, juveniles, and small subadults up to 1.3 m in length. Other group basking areas showed concentrations of subadult alligators capable of digging their own dens, but den sharing should not be ruled out. These large groups, ranging in size from 1.25 to 2 m of basking subadults were located around small gator pools in Flag Pond. Groups of 20, 22, 29, and 31 alligators were observed on several occasions when suitable conditions prevailed. Alpha and Beta males and breeding size females with no apparent offspring often basked singly on matted grass, floating logs, and living tree trunks.

As spring temperatures rose and pond waters increased the prey resources consisting of insect larvae and adults, mosquito fish, amphibians, and small lizards, the pod of neonates would return to the nursery areas chosen by the female the previous fall after the hatching. Most nursery areas were shallow meadows with varied vegetation for camouflage. Juveniles with sibling neonates were usually guarded as part of the pod as was evident in 1979 when the Palmetto resident female PF-1's 1977 and 1978 hatchlings formed one

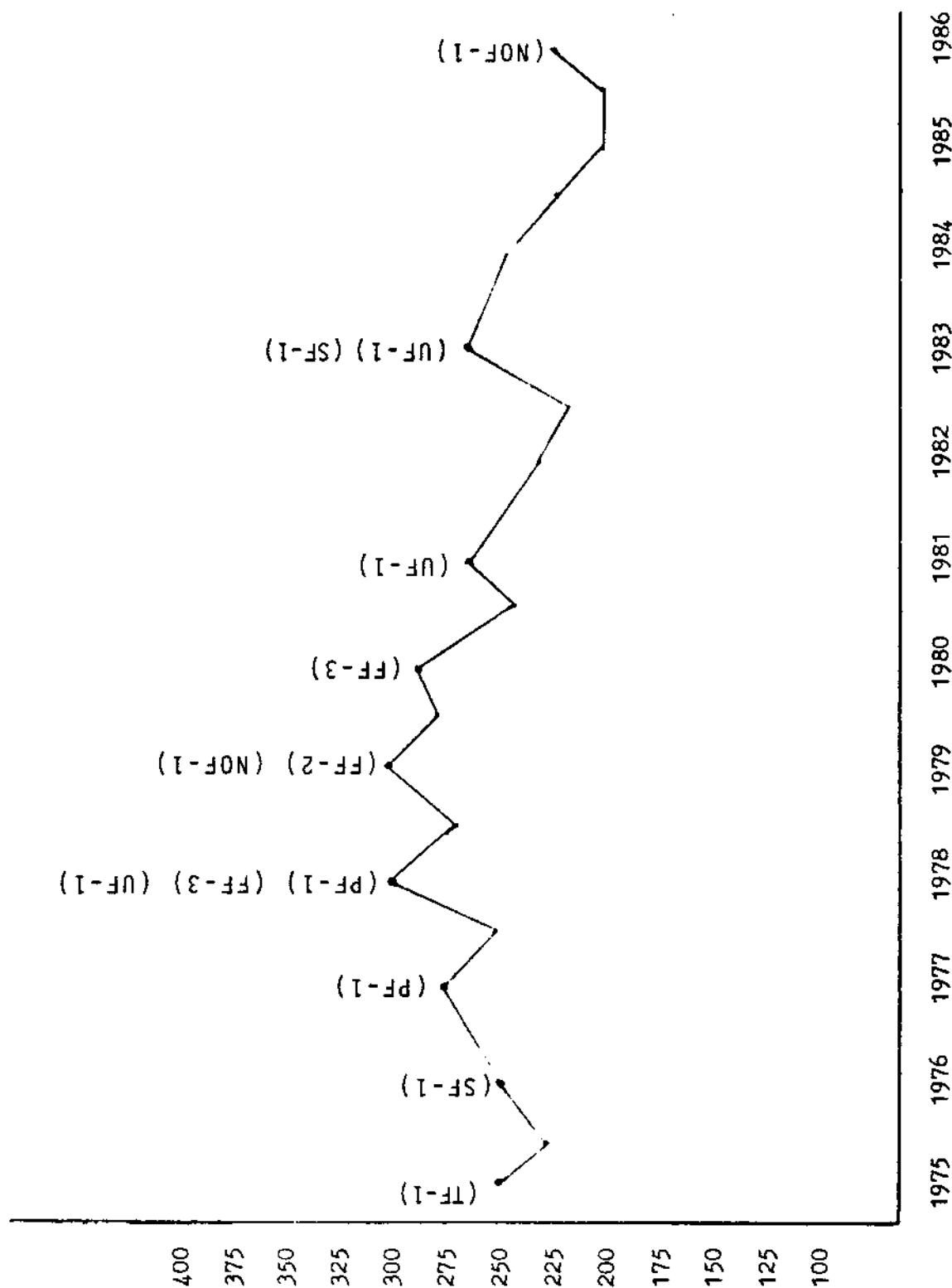


Figure 6. Population estimates of resident Wassaw Island alligators. () indicates the female that nested successfully that year.

pod. Other pods separated or were kept apart by the guarding female. Usher's resident female UF-1's 1978 juveniles relocated to other ponds when the 1981 neonate pod took over the nursery area. The same type of pod separations occurred in 1984 when the 1983 neonate pod took over the nursery area as 1981 juveniles were recovered in Otter Pond. Flag Pond female FF-3 nested successfully in 1978 and in 1980 and the dispersal of the 1978 pod was evident from the nursery area.

Environmental and Territorial Pressures on Juveniles and Subadult Alligators - Juveniles and subadults made up the peripheral residents of all fresh-water ponds as long as adequate water levels and prey were available. The 'peripheral' areas of the freshwater ponds were generally flooded, low-forested areas commonly referred to as overflow areas of ponds. These flooded swamp-like areas had no gator holes or large dens. Some small dens excavated by subadults were probably used by nomadic individuals more than as permanent type dens. The capture records indicate a large turnover in peripheral inhabitants and is most likely attributable to the trial and error period experienced by ranging subadults. As confirmed by the tagging project, subadults range from the winter den and spring basking areas into peripheral habitats of freshwater subadult population would relocate into the brackish ponds.

Prey Availability - Brackish ponds lack available prey until the high spring tides of late April or early May when thousands of finger size mullet, small shrimp, blue crabs and even tarpon enter through tidal creeks and become stranded until the following fall spring tide. Growing rapidly on the nutrient rich bottom of the brackish ponds, these prey resources provide the proper size food source and quantity for juvenile and subadult coastal alligators where no freshwater fish source is available. The importance of the brackish ponds as the ecological niche exploited by subadult alligators was confirmed by the 91 captures of 65 different alligators in the four brackish pond habitats.

Further subadult alligator captures confirmed their occasional exploitation of tidal pools, sloughs, and surf edge for crabs, schooling fish and dead, deposited bottom species that were washed ashore from commercial fishing trawlers. During one ten-day period in 1977, twenty individual alligators from 1 m to 1.8 m in size were located feeding in pools along a one mile stretch of the boneyard beach. Overall, 32 alligator captures took place on the Barrier Beach habitat of Wassaw Island. Numerous other track sightings on the beach were reported during the study period.

Tidal Marsh Exploitation - Marsh sightings of alligators began each spring with the arrival of Beta males in mid-May. Beta male #1 was captured heading toward the marsh near the south landing on 22 May 1977. Presumably too large at 2.3 m (TBL) to benefit from the finger size prey available in the brackish ponds, this and other large subadults and Beta males remain in the tidal marshes until fall cooling temperatures dictate their return to winter dens in freshwater pond embankments. Beta male #2 was captured in Teal Pond on 5 September 1979, four days after a hurricane had passed through plummeting temperatures and refilling the ponds. Beta male #3 was captured in Otter Pond Creek after returning from the tidal marshes on 10 November 1979.

Further information and observation of alligators in the tidal zone began with the captures of subadults feeding on striped mullet (*Mugil cephalus*) which school by the thousands out of the mouth of Mill Creek during outgoing low tides. On 30 June and 2 July 1978, two subadult males, MC78-1 and MC78-2, were captured while feeding in the shallow shoals formed by tidal deposits. Six to eight subadult and adult size alligators were seen by their red eyes which reflected off of hand held lights several times during the summer when below average tides occurred. Extremely low tides can occur due to westerly winds, moon and sun alignment, or as a combination. These lower tides nearly seal off the drainage from Mill Creek. Alligators were observed at night and early morning positioning themselves in shallow passages towards the oncoming current with their mouths 2 to 5 cm agape. As a school of mullet would swim through the small channel, alligators would jerk their heads rapidly sideways in an attempt to catch the fish. Mullet could be seen jumping frantically and turning around in the ambush area. Very few catches were observed, suggesting a low percentage success rate even within a confined area. MC78-1 continued trying to capture oncoming mullet as I approached wading with my headlamp and pole. The violent head jerking motions of

the alligator made noosing extremely difficult and several attempts were required before success was achieved.

During 1980 and 1981 it became more and more apparent that the five previous years of night-time searches and capture successes of the Wassaw Island alligator population had sensitized the freshwater inhabiting alligators. They began reacting to lights by quickly sinking and/or returning to dens. At the end of the 1980 research period, 170 different alligators had been identified on Great Wassaw Island.

Thirteen nights during June, July, and August, 1981, were spent observing alligators in the saltwater creeks and the adjacent marshes. Eighty-seven sightings of alligators were recorded. The smallest was estimated at 1.3 m, the largest 3 m. Patrolling the marshes during spring tides at night with a 100,000 candle power hand-held lamp, I observed only scattered individuals in the main boating channel of Odingsell, Wassaw and Romerly Creeks. As noted previously, six to eight subadult alligators had been observed at the mouth of Mill Creek during separate low and high water observations and eight to 13 large subadult alligators in the winding three km of navigable Mill Creek.

Another observation attempt revealed the most significant feeding behavior to date. To prove the ease of access to and from Mill Creek, my assistant and I canoed out of Otter Pond Creek on an incoming spring tide into the tidal marshes. From the end of Otter Pond, a narrow but distinguishable 40 m trail connected to a small finger channel of Mill Creek. The tide began receding as I reached deeper and wider channels. Mullet were observed pushing and plowing through the *Spartina* marsh grass towards deeper water from the surfacing mud flats. Mullet were seen and could be heard jumping from the shallow marsh beds towards the river channel. Striped mullet, a herbivorous and detritivorous feeding fish, penetrate high mud flats for nutritious deposits of decaying vegetation, and graze on epiphytes and epifauna from marsh grasses and other substrates (Collins 1985). As we approached the first subadult alligator, we found that it had positioned itself perpendicular to the marsh edge with its snout slightly penetrating the first grass stalks. Its mouth agape, body and tail angled down and out in deeper water, the alligator balanced itself against the outgoing current. Mullet were observed pushing, plowing, and jumping out of the higher grass covered mud flats past the alligator's position. The alligator showed no head side-jerking motion before submerging at our approach. Six more alligators from 1.5 m to 3 m (TBL) were observed, all in the same marsh edge position. The largest, an Alpha size male, had positioned himself at the mouth of a small draining tributary across from Mullet Creek intersection with Mill Creek. As his wide head bridged the narrow channel, mullet pushed through the grass edge of the channel, some jumping clear of the water directly over the head of the alligator. With only a slight head-jerk, an Alpha size male caught a 30 cm mullet at midbody. Lifting his head clear of the water, he tossed and rolled the mullet into position for a head-first swallow. The alligator, which hardly moved except in head position, resumed its original position and was not observed capturing another fish for the next hour, as mullet continued jumping and escaping from the small channel by the alligator at a diminishing rate. No other head jerks were observed at the time. An hour after the capture and feeding sequence, the tide had dropped below the surrounding high marsh and no mullet were seen moving toward the deep water channel for 25 minutes. The alligator submerged and did not reappear. No more alligators were seen in the short distance we travelled to the mouth of Mill Creek where it connects with Wassaw Sound. Three hours later, nearing low tide, four large subadults approached the shallow shoals of Mill Creek. Each positioned itself against the current in a shallow passage. Mullet, schooling toward the sound, could be seen and heard by the hundreds as they jumped and swam through the outflowing narrow passages. Soon rapid head-jerking was observed with two animals each successfully catching a mullet.

Beginning in 1981 and continuing through the 1986 research period, marsh boat trips were attempted during the nights of full and new moons. Particular effort was made to capture subadult alligators in Mill Creek in anticipation of recovering previously tagged individuals from interior habitats. During the numerous marsh excursions taken from 1981 to 1986, the receding spring tide feeding behavior was regularly observed.

Rangewide Movement - The main advantage of permanent tagging and dorsal caudal scute punch codes is the ability to recapture the marked alligators at any time in the future and have positive identification for comparing data. The projected hypothesis from early observations of the Wassaw Island alligator population was that possible migratory patterns might exist for coastal island alligator populations and that in search of prey, subadult alligators would conditionally leave the freshwater ponds of their winter dens and move into brackish ponds and eventually into the salt marshes and return again to the freshwater winter den site in a cyclic type pattern. Early evidence of rangewide movements came from the 91 captures of juvenile and subadult alligators in the brackish pond habitats. Barrier beach use by alligators searching for crabs, school fish, and washed-ashore, trawler-killed marine animals also was evident by the 32 beach capture records, and finally the additional capture information revealed from the tidal marsh exploiters.

The presence of Beta males in the tidal marshes is most likely attributed to two factors: one, territoriality of Alpha males forcing them from suitable habitat in freshwater ponds; and secondly, the unsuitable prey in the shallow brackish ponds. The smaller, 1.5 to 2.5 m subadults that make up the majority of marsh sightings benefit from the prey resources available in an otherwise marginal or unpreferred habitat. During 1984, S77-5 (1.5 m), F84-2 (1.86 m), F77-1 (1.75 m), and O79-6 (1.44 m) were all captured in Mill Creek. F77-1 had been captured in four different habitat locales since its initial capture in Flag Pond in 1977. S77-5, F77-1 and F84-2 were all initially captured in freshwater ponds. O79-6 was captured in the brackish Otter Pond in 1979. Here was increasing evidence of the use of the salt tidal zone as an ecological niche important to the growth and survivability of a coastal island American alligator population. During 1985, D85-1 (1.62 m) was captured in Mill Creek, further suggesting a preference for a larger prey source over the smaller source provided in the brackish environment of Dike Pond. This past season (1986), MC78-1 (2.07m) was recaptured in the Mill Creek tributary of Mullet Creek. Because eight years had passed since MC78-1's initial capture, it is possible that the tidal marshes provided an available food source necessary to bridge the gap for large subadults and Beta males until a suitable freshwater habitat could be found.

Long Distance Recoveries - Female S77-2 (1 m TBL) was first captured in the peripheral southern end of South Pond and was captured again 13 days later on the South End Beach (straight line distance 6.5 km) with jumping cactus spines impaled in her skin from crossing the transitional dune ridge habitat. The greatest distance covered by a recaptured Wassaw alligator was recorded in the 1980 study season. B80-1 female (1.5 m TBL) was captured and tagged on the central barrier beach of Wassaw Island. Fifteen days later an employee with the South Carolina Wildlife Services captured the same tagged alligator as it crossed a dirt road 1.6 km west of the beach on Hilton Head Island, South Carolina (straight line distance between capture sites was over 50 km). In 1982, O82-1 (1.25 m TBL), originally caught in Otter Pond, was recaptured three months later by the Georgia Department of Resources on Wilmington Island (total straight line distance travelled was 12 km). Another alligator captured in Otter Pond in 1982, O82-9 (0.91 m TBL), was recaptured in 1984 using a flap gate trap developed by A.C. Pooley in Natal, South Africa. The colored plastic rings in the dorsal caudal punched scutes alerted a Talahi Island resident to his new guest in his private catfish pond. This alligator (O82-9) had moved 13.5 straight line km from its original capture sight two years earlier.

The recapture record for many individual Wassaw alligators shows a limited distance covered when recaptured. However, the island's complex and varied habitat zones are compact and close. There is strong evidence of ranging behavior in search of adequate habitat and proper size prey availability. Table 1 lists recaptures with habitat changes and the covered distances.

DISCUSSION

The barrier islands of Georgia's Atlantic coast offer a variety of habitats that are exploited by different size alligators. On Wassaw Island neonates, juveniles, and even subadults were observed emerging from the communal winter dens of adult nesting females. The adult males and the remaining subadults

hibernated from December to March in separate dens. All winter dens were in the freshwater habitats. By establishing the location of the Wassaw Island alligator population in the freshwater habitats when they emerge from the winter dens for basking, their movements were determined from the capture data. Neonates preyed on amphibians, mosquito fish, insects and other arthropods that were abundant in the flooded marshes of spring and fall. Gator holes as reported previously (Meyer 1975) serve as the last freshwater sources on the barrier islands. Dominate males and females capture prey that comes to drink at these water holes (four deer carcasses and one skull with alligator teeth marks were found during this study).

The movements of alligators of Wassaw Island were attributed to several factors. Fluctuating water levels in freshwater ponds have prevented the successful establishment of freshwater fish that are available throughout a majority of the alligators range (Neill 1971). The seasonally abundant fish and crustaceans in brackish habitats on coastal barrier islands were used as the primary food sources for juvenile and < 1.5 m (TBL) subadult alligators. Subadult alligators observed on the barrier beach in tidal pools left by the receding tide demonstrated a feeding method of raking with open jaws through the loose sand at the bottom of the pools for locating and capturing blue crabs. Carrion feeding, on fish and crustaceans deposited by wave action after being thrown overboard from commercial trawlers, was also observed among the barrier beach alligators. Subadult alligators > 1.5 m (TBL) and Beta males exploited the tidal marshes for larger prey such as striped mullet. By blocking or constricting the exit areas of feeding and schooling mullet, alligators were able to snap at the concentrated fish, increasing the possibilities of capture. The Nile crocodile also exhibits a feeding behavior for mullet species at Lake St. Lucia in Natal, South Africa. Pooley and Gans (1976) reported that crocodiles cooperate by forming a semi-circle where a channel empties and the crocodiles catch the incoming fish as they pass through the ranks.

The capture and tagging of the subadult alligator population established over the ten year study period that the coastal alligators were forced to adapt to new habitats and that some food sources required increasingly more sophisticated capture techniques as the alligators matured. The demand by the increasing human population for more waterfront and coastal island properties will inevitably cause additional strain on the resident alligators. Emigrating individual alligators from the Wassaw population have already been recaptured in human residential areas where new deep water habitat was developed.

Human population pressures on the coastal islands are expected to continue into the next century. Government planners and private developers should set aside adequately protected nesting and nursery areas so that the increasing alligator population won't become a dangerous conflict to the new human residents. However, care must also be taken not to destroy the corridors and brackish systems necessary for the movement and survivability of the subadult alligator population of Georgia's Atlantic coastal zone.

ACKNOWLEDGEMENTS

I would like to acknowledge the following organizations for their financial and logistical support: Atlanta Zoological Society; Department of Herpetology, Zoo Atlanta; Wassaw Island Trust; U.S. Fish and Wildlife Service; Savannah Science Museum and the Oatland Island Educational Center. Gratitude is also expressed to R. Howard Hunt, Curator of Herpetology, Zoo Atlanta for his guidance and valuable assistance throughout this project. Special thanks are extended to Alex Barbee, Martin Perry, Charles Warnock, John Crawford, Darryl Smith, Guerry Beam, Tony Cope, Randy Booker and Eric Laudin for their enthusiastic support and participation in collecting field data. Appreciation is also expressed to participants of the Savannah Science Museum's Carretta Research Project on Wassaw Island, staffs of the Oatland Island Education Center, Skidaway Institute of Oceanography and the Marine Extension Service of the University of Georgia for their assistance on field expeditions. Special thanks to Virginia Anderson for some of the drawings included in this paper and to Nancy Tamarack, Sue Cole and Jim Sheehan for their editorial comments and manuscript preparation.

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Table 1. Recorded Habitat Changes of Wassaw Island Subadult Alligators.

| Identity Code | Original Capture/Date | New Habitat/ Recapture Date | Distance Covered |
|---------------|-------------------------|--------------------------------|------------------|
| I76-2 | Island Interior 25-5-76 | South Pond 28-4-77 | 1.8 km |
| | | Barrier Beach 18-7-77 | 4.8 km |
| | | Otter Pond 23-8-84 | 1.1 km |
| S77-2 | South Pond 28-4-77 | Barrier Beach 11-5-77 | 6.5 km |
| Beta Male #1 | Island Interior 22-5-77 | Wassaw Creek 28-7-84 | 0.7 km |
| S77-5 | South Pond 25-5-77 | Mill Creek 30-6-84 | 5.5 km |
| F77-1 | Flag Pond 7-6-77 | Cedar Pond 06-9-78 | 1.2 km |
| | | N. Otter Pond 11-9-78 | 0.6 km |
| | | Mill Creek 27-8-84 | 1.5 km |
| B77-2 | Barrier Beach 16-7-77 | Otter Pond 13-9-86 | 0.8 km |
| B77-4 | Barrier Beach 17-7-77 | Cedar Pond 02-6-79 | 1.6 km |
| B77-16 | Barrier Beach 24-7-77 | South Pond 26-4-80 | 6.3 km |
| P78-2 | Palmetto Pond 25-5-78 | Barrier Beach 15-6-82 | 3.4 km |
| I79-1 | Island Interior 11-5-79 | Wassaw Creek 20-7-83 | 3.7 km |
| I79-2 | Island Interior 04-7-79 | South Pond 11-8-79 | 0.2 km |
| O79-6 | Otter Pond 02-8-79 | Mill Creek 10-10-84 | 1.4 km |
| U79-10 | Usher Pond 06-8-79 | Otter Pond 29-8-83 | 1.6 km |
| U79-11 | Usher Pond 14-8-79 | South Pond 06-7-84 | 1.0 km |
| NO80-7 | N. Otter Pond 28-8-80 | Otter Pond 29-6-82 | 0.1 km |
| NO80-11 | N. Otter Pond 28-8-80 | South Pond 28-8-80 | 3.2 km |
| NO80-14 | N. Otter Pond 28-8-80 | Otter Pond 26-7-85 | 0.1 km |
| U81-1 | Usher Pond 15-9-81 | Otter Pond 29-8-83 | 1.6 km |
| F84-1 | Flag Pond 21-5-84 | South Pond 21-7-84 | 2.4 km |
| F84-2 | Flag Pond 30-5-84 | Mill Creek 27-8-84 | 1.4 km |
| D85-1 | Dike Pond 26-7-85 | Mill Creek 14-10-85 | 2.6 km |

THE CAIMAN OF THE PANTANAL: PAST, PRESENT, AND FUTURE

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The Pantanal is a complex region which lies in the basin of the Rio Paraguai, in the Brazilian states of Mato Grosso and Mato Grosso Du Sul. The region is approximately 100,000 km², and is largely composed of permanent swamp, seasonal swamp, gallery forest, marginal scrub, savannah, and semi-deciduous forest. The Pantanal, for the most part, is less than 100 m above sea level. The climate ranges from extreme drought to rainfall in excess of 1200 mm, which falls between December and February. Temperatures may range from nearly 0° C in the dry season to over 40° C during the rainy season. While endemic species are widespread, they are few in number. The Pantanal caiman or Jacare, better known as the Yacare caiman, *Caiman crocodilus yacare*, is the only crocodilian which inhabits the Pantanal proper (Medem 1983, Prance and Schaller 1982, Schaller and Crawshaw 1982; Fig. 1).

Because the hide of the Yacare caiman bears wider flank regions (Fig. 2a, 2b; the portions most often used in the manufacture of products) than the other races of caiman, it has been the more desirable species and the mainstay of the commercial caiman leather trade. In the United States alone, the caiman hide and product trade, which includes the Yacare, amounted to over ten million dollars in declared value for the first nine months of 1986 and included 355,560 items. Caiman skins, including Yacare, make up at least three-quarters of the estimated 1.5 to 2 million crocodilian skins in annual world trade. However, Yacare only occur in southern Brazil, eastern Bolivia, northeastern Argentina, Uruguay and Paraguay (King and Brazaitis 1971, Brazaitis 1973, Medem 1983). Paraguay and Bolivia are the major exporters of Yacare hides (Hemley 1979).

Yacare caiman are listed under Appendix II under CITES and as an endangered species under the U.S. Endangered Species Act, and are banned from the U.S. trade since June, 1970. In 1971 and in 1974, Karlheinz Fuchs, in non-scientific industry trade journals (Fuchs 1971, 1974), described several races of Yacare caiman (*C. c. paraguayensis*, *C. c. matogrossoensis*) as *nomen nudum*. They were added to the checklist of crocodilians by Wermuth and Mertens (1977), and were subsequently repudiated by Medem (1983), Frair and Behler (1983), and Mayer and Ross (in prep.). Although these *C. c. yacare* synonyms were not adopted as valid subspecies, exempt from the endangered classification of the USA, the names were incorporated into the 1983 official CITES Identification Manual. Today, prompted by industry pressure and the taxonomic confusion which has been raised, and which could have serious ramifications on the management and conservation of the species, the Yacare caiman, particularly populations from Brazil, Paraguay, and Bolivia, are the subject of intensive taxonomic and populational investigation. At this time, the species continues to be banned from U.S. trade. Anticipating the possible availability of large numbers of Bolivian and Brazilian Yacare skins in a climate of relaxed controls, and fueled by the recent infusion of Venezuelan "baba" (*C. c. crocodilus*) skins into the market, the crocodilian skin leather trade launched a major fashion campaign to promote crocodilian skin products in 1986-1987.

The Yacare of the Pantanal is highly subject to any increased demands for Yacare hides. Yacare populations in Brazil, which are totally protected under Law 5197 since 1967 (Fuller and Swift 1984) largely inhabit the Pantanal, a region bordered by Bolivia and Paraguay. Despite complete protection, Brazilian Yacare have historically been taken illegally in large numbers by Bolivian and Paraguayan traders. Unfortunately, illegal hunting practices often take place during periods when the animals are most susceptible to drastic depletion. Animals congregate in numbers in small shallow cattle watering ponds during the dry season. Although areas may be remote and inaccessible during the wet season, such ponds



Figure 1. Bold dark blotches on the sides of the jaws and an overall dark body coloration are typical of adult *Caiman crocodilus yacare* in the Pantanal.



Figure 2a. The region of the body between the fore and hind limbs of *Caiman crocodilus yacare* is particularly wide and bears aesthetically pleasing round scales. These "flanks" are often the only portion of the animal which is utilized, while the remainder of the wild killed animal is discarded.



Figure 2b. The tanned "flank" may include the side of the body, short portions of the legs, the throat, and the base of the tail. Flank skins make up the bulk of the caiman leather trade, and are used to make belts, watchbands, shoes and wallets. In 1986 and 1987, whole belly skins of caiman from the Pantanal began to appear in great numbers as imports into the United States. All are seized by the U.S. Fish and Wildlife Service. Caiman belly skins most often were used in the manufacture of luxury handbags and are often labeled as ALLIGATOR.

are easily accessible by truck during the dry season. Light aircraft can also land virtually anywhere in the Pantanal to pick up illegally taken skins, and fly directly out of the country to ports in Bolivia and Paraguay. Females with young are particularly susceptible, in that lone females are attending young in small easily accessible nursery ponds during the heavily hunted dry season (Cintra 1985, Crawshaw and Schaller 1980). The effect of these illegal hunting practices on the Pantanal caiman is evident.

In cooperation with the Instituto Brasileiro de Desenvolvimento Florestal (IBDF) and Long Island University, New York, and with the support of WWF-U.S.A. and the New York Zoological Society, I visited the Pantanal in October/November 1985 on a cursory preliminary survey of *Yacare* populations. Areas previously surveyed by Schaller and Crawshaw in October 1978 were re-assessed. Populations were sampled in a transect of the Pantanal from north to south, and west to the Bolivian border. Although the results are not conclusive, based on the very short survey period, they are indicative of the current situation. Few animals found were larger than 1.2 to 1.8 m in length, considerably smaller than the 2.5 m to 2.8 m size potential for the species. In most populations of adults sampled, and observed by Brazilian biologists, males often outnumber females 4:1. In one pond, one female dominated a pond containing over 30 males. In contrast, a sex ratio of 1:1 was not uncommon in populations of sub-adult animals less than one meter in length. Along one 14 km stretch of road bordered by several cattle ponds, Schaller and Crawshaw (1982) estimated a *Yacare* population of 2000 to 3000 animals. In October 1985, we found the ponds to contain between 25 to 50 animals, and the entire stretch to contain fewer than 500 to 600 animals, mainly in locally protected isolated pools.

Although poachers also take anaconda, spotted cats including jaguar, plus otters and tapirs, they frequently operate unchallenged. Poachers are well equipped and well organized. Even when apprehended, they often escape imprisonment and have fines and the value of confiscated skins reimbursed by the hide buyers. New roads for a developing tourist trade are opening otherwise inaccessible regions. Brazilian wildlife authorities are doing an exemplary job in attempting to stem the flow of illegal skins, but they are working under difficult conditions with little money, poor judicial support, and little equipment. One officer confided that he had called off an attack on a known poaching operation when he realized his men had an average of three bullets per person. Landowners, except for a brave few, do not interfere with poaching unless the poachers take cattle or salt stores.

The future of the *Yacare* in the Pantanal, as well as the economy of this unique region, could be permanently enhanced by the sound management and conservation of this important wildlife natural resource. Landowners as well as several government agencies have begun to develop pilot projects which would utilize the protected wild populations as a basis for caiman ranching operations. The local fishing industry, and the developing tourist trade may become positive complementary industries. Effective conservation may lie not only in law enforcement, but in an awareness by local peoples in the Pantanal that the protection of the wild population, particularly nesting females, can result in a renewable "cash crop" of young animals for Brazilian caiman ranches. Such an industry has a long way to go. To be economically feasible, a ranched caiman must produce a total estimated return of about \$200 in hide, meat, bone, and tourist revenues. Hide dealers pay only U.S. \$5 to \$10 per skin. Thus, the illegal trade must be stopped if a new ranching industry is to prosper. At the present time, ranching efforts are in their infancy (Luxmoore et al. 1985) and range from serious business investments and the development of state of the art husbandry techniques, to operations such as were seen in Miranda in Mato Grosso do Sul. There, when it was learned that Brazilian authorities may open a hunting season, a new sign was erected in anticipation, naming the ranch "caiman ranch." When I asked where the rearing areas were, the reply was, "The whole ranch. When the time comes, we will kill all of the wild ones."

The long term future of the Pantanal *Yacare*, and perhaps the economy of local peoples, may best be served not simply in estimating the extent of the endemic *Yacare* population and harvesting it to its maximum, but in making provision for and supporting the growth of a new Brazilian industry which encompasses the management and conservation of the wild population, ranching, tanning, fishing, marketing and tourism. Such an industry might well be of infinitely greater long range benefit to many more of the Brazilian people and may better preserve the Pantanal caiman.

ACKNOWLEDGMENTS

I would like to express my thanks to Dr. David Challinor, Smithsonian Institution; World Wildlife Fund - U.S.A.; The New York Zoological Society, particularly John Behler; Dr. Dennis Curley and Long Island University; Jordan Wallauer, Peter Crawshaw and IBDF, Brazil, for help, support, and hospitality during the course of this work. I would also particularly like to express my thanks to my Brazilian colleagues in IBDF, Carlos Yamashita and Renato Cintra who provided me with field assistance, friendship, and an "orthopedic road." There were many others in Brazil, too numerous to mention. Lastly, to my wife Dr. Myrna Watanabe, for her extreme patience and counsel -- my most valued colleague.

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A COMPARISON OF SIZES OF CAIMAN IN HUNTED AND NON HUNTED AREAS IN THE BRASILIAN PANTANAL

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ABSTRACT - Sizes of hunted caiman (based on snout-vent length of confiscated skins) in the Brazilian Pantanal were compared with sizes of animals in an unhunted population. There is a significant difference between the size distribution of skins of hunted animals and sizes of animals available in the unhunted population. The hunters show a clear preference for caimans larger than 80 cm snout-vent length.

INTRODUCTION

The Paraguayan caiman (*Caiman yacare*) may be the most heavily exploited crocodilian in the world, but we know almost nothing about the effect of hunting on populations of this species. We can however, get an idea of the sizes being hunted from the sizes of confiscated skins.

The aim of this paper is to present data on the size of caiman being hunted in the Brazilian Pantanal and compare these with data of sizes of animals in an unhunted population.

METHODS

I studied the caimans along the transpantanal road in the Municipality of Poconé (56° 59' West, 17° 16' South). The Pantanal is a large area (100,000 km²) of seasonal swampland in southwestern Brazil.

During the dry season the caiman form large concentrations in natural and artificial pools along the road. Individuals (200) of different sizes and both sexes were randomly captured and measured.

To get an idea of the size of caiman being hunted, I measured a random sample of skins confiscated by IBDF (the Brazilian wildlife agency), near the Bolivian border. I measured 95 of the approximately 600 skins that they had confiscated.

Because the hunters cut around the neck and in front of the vent it was impossible to measure snout-vent (SV) length directly. I estimated the snout-vent length and the distance between the front and back legs in entire skins. Unfortunately, I had no entire skins of *Caiman yacare* and so I estimated the relationship based on 61 entire skins of the closely related species, *Caiman crocodilus*, which were confiscated by IBDF of Manaus. I used the following equation:

$$SV = \frac{DBL + 1.75}{0.49}$$

Where DBL = Distance between front and back legs; ($1.75 = a$ and $0.49 = b$ values of the linear regression of DBL on SV) made for *Caiman crocodilus* skins ($r = 0.94$).

RESULTS

There is a significant difference between the size distribution of skins of hunted animals and sizes of animals available in the unhunted population. (Fig. 1).

It is unlikely that the sizes of animals in the hunted population are larger than animals in the unhunted population. Therefore the hunters are showing a clear preference for caimans larger than 80 cm snout-vent length.

This small sample suggests that the populations are not being reduced by the hunting. However, the only valid way to determine the effects of hunting is to directly survey the hunted population. This is not being done in Brazil. In a postal survey of the 14 IBDF agencies, Rêbello and Duarte (1984) recorded 8,622 crocodilians among 31,165 reptile skins. And Duarte and Rêbello (1985) recorded 26,880 carnivore skins just in the IBDF office in Rio de Janeiro, but they were not sure if these skins come from the rest of country or due to more efficient confiscation in that state. Even the indirect method of assessing the sizes of hunted skins has not been used in Brazil, since the study by Rêbello and Magnusson (1983). Most skins of crocodilian and other wild life confiscated are destroyed with minimal or no documentation. Just the IBDF office in Manaus will burn about 3000 *Caiman crocodilus* skins. Although there are IBDF Projects to register the confiscated skins of endangered species, it is not well controlled and organized by each regional agency, and the data is not available to the Scientific Community.

ACKNOWLEDGMENTS

I thank Bill Magnusson for helpful comments on the manuscript. Aroldo Klein and Adalberto Filho (IBDF-Cuibá) helped me with the access to *Caiman yacare* skins. Manasses Martins and José Guilherme Lima helped me with skins measurements. Angelo de Lima Francisco and Antonio Carlos Hummel (IBDF-Manaus) helped me measure *Caiman crocodilus* skins. Valdeira M^a J. Azevedo typed the manuscript.

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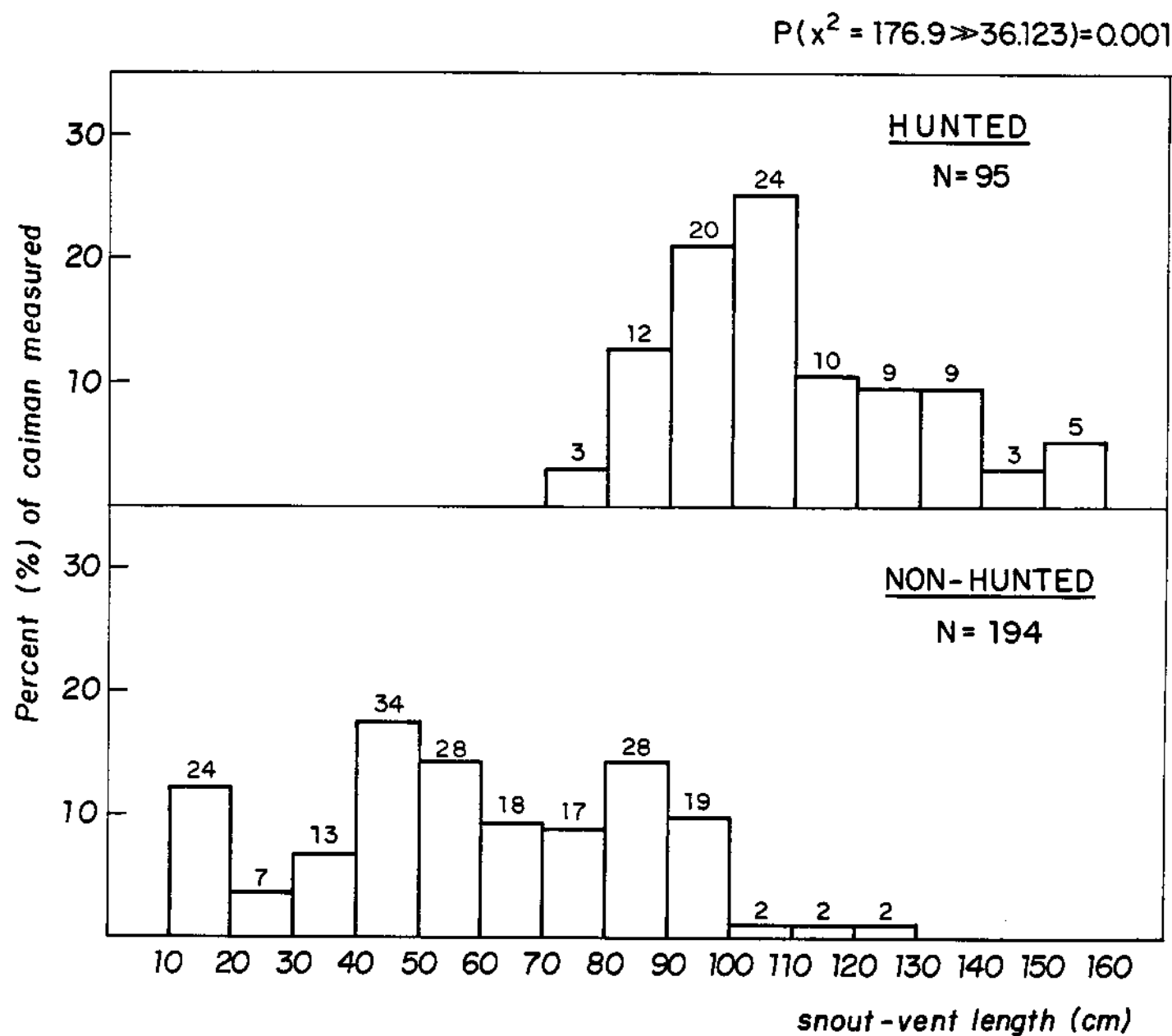


Figure 1. Comparison of size (by snout-vent length) between hunted and non-hunted caiman from two different areas in the pantanal.

**THE CAIMANS OF BOLIVIA:
A PRELIMINARY REPORT ON A CITES
AND CENTRO DE DESARROLLO FORESTAL
SPONSORED SURVEY OF SPECIES DISTRIBUTION AND STATUS**

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ABSTRACT - Between June 1986 and May 1987, a survey of the species and distribution of Bolivia's caimans was conducted, including rough estimates of relative abundance of both species and habitat, species utilization and status. Preliminary results suggest that as a consequence of commercial hunting for their hides, *Caiman latirostris* is in immediate danger of extinction; *Melanosuchus niger* is more widely distributed but also is in danger of extinction; and *Caiman yacare* remains widely distributed despite being badly mismanaged. *Paleosuchus palpebrosus* and *Paleosuchus trigonatus* are not commercially hunted and remain locally abundant. Utilization of the caiman resource and the status of wildlife conservation in Bolivia is reviewed. To address regional conservation problems, two resolutions are offered for consideration at the 6th Meeting of the Conference of the Parties to the CITES in Ottawa, Canada, 12-24 July 1987.

INTRODUCTION

This survey of Bolivia's caimans was undertaken at the request of the CITES Secretariat, and conducted under the terms of a formal Convenio (= Memorandum of Understanding) between the Secretariat, on behalf of CITES, and the Centro de Desarrollo Forestal (CDF), on behalf of the government of Bolivia. Vida Silvestre, Parques Nacionales, Caza y Pesca (= Wildlife, National Parks, Hunting, and Fishing) is a department of CDF. The Bolivian survey is part of a larger, tripartite, regional effort, aimed at developing and implementing a comprehensive program for conserving the caimans of Bolivia, southwestern Brazil, and Paraguay. The immediate purpose of the survey was to verify what species of caiman occur in Bolivia and to determine the exact distribution of each. This information will enable the government of Bolivia to assure that its management authority issues CITES country of origin export permits solely for species of caiman that are found in Bolivia.

In addition, the survey is the first phase of an effort to develop a program that monitors the impact of hide exports on the wild populations as required under Document 6.2 of the Buenos Aires Conference of the CITES Parties. During the survey, populations of caimans were identified which could be studied in a second phase of the project to document the ecology and natural history of each species. Data from those studies will provide the scientific base upon which a program for the conservation management and sustained utilization of the caiman resource can be built, thereby satisfying Doc. 6.2.

METHODS

The species and subspecies of caimans differ in color, morphology of the skull, the numbers of scales on different parts of the bodies, and in various biochemical attributes. In order to verify the specific characteristics of Bolivia's caimans, it was necessary to collect and preserve voucher specimens, which could be used not only by the present research team, but which also would be available to other researchers, who might wish to verify our findings. All the specimens from the tripartite study in Bolivia, southwestern Brazil, and Paraguay, are being shipped to the Florida State Museum (FSM)*, Gainesville, Florida, U.S.A. In the FSM, the morphology and biochemical characteristics of the voucher specimens will be studied by a single team of researchers, thereby minimizing differences that might inadvertently be introduced if specimens from each of the three countries of origin were studied by separate teams of researchers. When the study is complete, all the specimens will be deposited in the systematics research collections of natural history museums, where they will be available to future researchers. At least 50% of the specimens will be returned to natural history museums in the countries of origin.

The extent and suitability of potential habitat at most collecting sites were explored during the day, but collecting was done at night when caimans are more easily located by their eyeshine reflected in the beam of a spotlight. Every effort was made to collect specimens as humanely as possible; smaller specimens were captured alive by hand and larger specimens were killed instantly by shooting them in the brain. Specimens captured alive were euthanized by lethal injection. Specimens smaller than 1.5 m total length usually were preserved whole, while larger specimens usually were flayed (with attached skulls) after being measured, weighed, and sexed. All specimens were individually tagged and preserved in 10% formalin. After shipment to the FSM, all the specimens were transferred to 60% isopropyl alcohol. In the field, data were recorded on the exact locality where each specimen was collected, as were data on habitat. Blood, liver, heart, muscle, and skin tissue samples were collected from approximately 20% of the specimens after they were euthanized but before preservation. The tissues were dried for later biochemical analysis. Data from these analyses will characterize the various taxa and populations and complement the data from the morphological studies. A total of 3 voucher specimens, hides with regional locality data, were contributed by hide buyers, and 2 additional specimens came from illegal hides, from known localities, seized by CDF forest guards.

Attempts were made to estimate the size and/or density of selected wild populations by counting the number of caimans, e.g., the animals seen or reflected eyeshine, seen per km of river or lagoon shoreline. Some rivers and lagoons were sufficiently small to allow both shores to be scanned from a boat in midstream. Other rivers and lagoons had mudbanks or rockbars that prevented close approach to one shore or were so wide that only one shore could be scanned. For this reason, population densities were estimated on the basis of km of shoreline rather than km of river. By virtue of their narrowness, roadside borrow pits and ditches are an exception; their populations are estimated on the basis of km of length. Having no large scale maps or aerial photographs of the particular waterways, we lacked accurate means of measuring the distances covered. As a consequence, these findings are presented solely as a crude index of abundance and not as incontestable census figures.

Habitat types were quantified by means of aerial transects, i.e., recording how long it took each major habitat type to pass the wing strut of a Cessna 185 flying approximately 140 m above the ground, and then using those data to estimate total available habitat.

Bolivia is so large and has so much potential habitat that it would be impossible to sample every population of caimans with 5 years of effort, much less with only 6 months in the field. Faced with that reality and the concurrent need to uncover every species of caiman that occurs in Bolivia, the survey team made an effort to collect specimens from upstream, downstream, and in between, in every major river system, and from every lake region, network of marshes, and principal wetlands complex. If unexpected

* In 1988, the name was changed to the Florida Museum of Natural History.

taxa or unusual populations were uncovered in these samples, additional collections were made in the particular region and in surrounding drainage systems.

Illegal cocaine operations made collecting impossible in some regions and difficult in others -- in September 1986, Noel Kempff Mercado, Director of the Santa Cruz de la Sierra Zoo, and two companions were killed when they stumbled onto a cocaine extraction operation in the Serrania Huanchaca of eastern Santa Cruz. Because of these illegal operations, it was not possible to collect extensively in the Chapare region (the lowland portion of the Department of Cochabamba, and adjacent portions of the Department of Beni), involving the upstream sections of the Mamore drainage. Collections also were not as extensive as desirable in the upper Beni river drainage (in southwestern Beni).

Interviews with caiman hunters, hide buyers, ranchers, and knowledgeable local residents provided much valuable data on the distribution and natural history of various caimans.

F. Wayne King and Fred G. Thompson (Florida State Museum, Gainesville, Florida, U.S.A.) and Carlos Alvarez and Dante H. Videz Roca (CDF, Santa Cruz, Bolivia), began the survey on 14 June 1986 in the central and eastern regions of the Department of Santa Cruz, and continued fieldwork in the northern and southern regions until late July. Thompson and Videz surveyed south through the Departments of Chuquisaca and Tarija during the last week in July. King, Thompson, and Videz, surveyed north into the Departments of Beni and Pando in August, ending there on 28 September. Jose Labao Tello (Maputo, Mozambique), who was conducting a survey of the felids of Bolivia on behalf of CITES and CDF, assisted the caiman survey team in Beni and Pando in August and September. From 7 to 21 January 1987, King and Videz resumed the survey in the Departments of Beni and La Paz, and were assisted briefly by Mario Challapa Zapata (CDF, Beni, Trinidad).

Finally, from 18 to 26 May 1987, the fully tanned and finished caiman hides in the warehouses of the six licensed members of the Asociación de Industriales de Cueros de Saurios (ASICUSA) were inventoried by King, Videz, Peter Brazaitis (New York Zoological Society, Bronx, New York 10460, U.S.A.), Juan Villalba-Macias (TRAFFIC/SudAmerica, Montevideo, Uruguay), Candido Pastor (CDF, Cochabamba), and Heriberto Cardozo (CDF, Santa Cruz).

RESULTS

Since morphological and biochemical analyses of all the specimens collected in Bolivia and Paraguay have not been completed, and the Brazilian specimens are only now being collected, the results reported here are to be considered preliminary. Identifications might change when the analyses are completed. In addition, apart from using the specific name *Caiman crocodilus* rather than the synonym *Caiman sclerops*, the nomenclature used in this report follows that used by the last revisor of South American caimans, Professor Federico Medem (1981, 1983) in recognizing:

- Caiman crocodilus* (Linnaeus 1758).
- Caiman crocodilus apaporiensis* Medem 1955
- Caiman crocodilus chiapasius* (Bocourt 1876)
- Caiman crocodilus crocodilus* (Linnaeus 1758)
- Caiman crocodilus fuscus* (Cope 1868)
- Caiman latirostris* (Daudin 1802).
- Caiman latirostris chacoensis* Freiberg and Leitao de Carvalho 1965.
- Caiman latirostris latirostris* (Daudin 1802)
- Caiman yacare* (Daudin 1802).
- Melanosuchus niger* (Spix 1825).
- Paleosuchus palpebrosus* (Cuvier 1807).
- Paleosuchus trigonatus* (Schneider 1801).

Wermuth and Mertens (1961, 1977), King and Brazaitis (1970), Groombridge 1982), and Wermuth and Fuchs (1983) treat *C. yacare* as a subspecies of *C. crocodilus*, but virtually no justification is given. Schmidt (1928), Donoso-Barros (1974), and the last revisor of the caimans, Medem (1960, 1981, 1983), recognized it as a full species and described its distinctive morphology. While he did not propose separating it as a full species, Densmore (1983), showed that there was more evolutionary distance between *yacare* and the other subspecies of *C. crocodilus* than there was among those other subspecies, evidence which tends to support separation as a species.

Medem (1983), did not consider *Caiman crocodilus matogrossiensi* and *Caiman crocodilus paraguayensis* to be recognizable subspecies. Morphological and biochemical analyses of the specimens collected by the Bolivia, southwestern Brazil, and Paraguay surveys may prove *matogrossiensi* and *paraguayensis* to be good subspecies, but we are following Medem until the analyses have been completed.

Species: In his 1973 survey of the caimans of Bolivia, Medem (1983), confirmed the presence of *C. latirostris*, *C. yacare*, *M. niger*, *P. palpebrosus*, and *P. trigonatus* (Figs. 1-5). Though Bolivian officials have issued CITES country of origin permits for the export of *C. c. crocodilus* hides, Professor Medem did not find this taxon in Bolivia. He did report it (Medem 1983), from upstream tributaries of the Rio Madre de Dios in Peru, and suggested hybridization between *yacare* and *crocodilus* should occur on the upper and middle reaches of the Rio de Madre de Dios upstream of the northwestern border of Bolivia. The present survey largely confirms Professor Medem's findings.

Caiman latirostris = Overo and Caiman del Chaco. The Overo is the most critically endangered species of caiman in Bolivia. Although Medem (1983) reported this species from localities in both the Paraguay drainage (in the Paraguai and Pilcomayo rivers), and in the Amazon drainage (in the Itenez, San Miguel, Mamore, Beni, Orthon, and Piray rivers), he found it so endangered that it was poorly known even to the professional caiman hunters. Thirteen years later, the species has been pushed so much closer to extinction that, despite our visiting most of the localities reported by Medem, the Bolivian survey teams only found the Overo in the Pilcomayo river (Fig. 1)¹. However, the teams did encounter a few caiman hunters and hide buyers, who knew the Overo and reported its presence in the Itenez, Mamore, and Beni rivers. Every one stated it was extremely rare. One buyer reported that the Overo used to be abundant in the Paraguai river, and occurred, but was never numerous, in the Itenez. To illustrate his statement, he reported that 20 years ago, a shipment of hides from the Itenez would include approximately one Overo, *C. latirostris*, hide for every 5,000 Lagarto, *C. yacare*, hides. In recent years, he has not seen even one Overo hide from the Itenez. By 1979, the species had become endangered in Argentina as well. Fitch and Nadeau (1979) surveyed the Argentine Departments of Mburucuya, San Miguel, and Concepción of Corrientes found 1,200 *C. yacare*, but only 2 *C. latirostris* (0.16%). They report that Overo hides accounted for 2.5% of the commercial hides sold because the hunters sought out the species for its more valuable hide.

In Bolivia, the habitat of the Overo consists of rivers, oxbow lakes, and lagoons with abundant emergent or floating vegetation along the banks. It occurs together with *C. yacare*. It seems to prefer quiet water habitats. The species is too endangered to determine whether or not there was any habitat partitioning between it and *C. yacare* as has been observed in Argentina (Nadeau and Fitch 1980).

The species already is commercially extinct in Bolivia; hunters and buyers almost never see it and the species cannot support any further hunting pressure. Clearly, it deserves the protection afforded by its placement on CITES Appendix I. If efforts are not made soon to conserve it, in few years it will become

¹ In his 1987 report to CITES on THE SITUATION OF THE WILD CATS (FELIDAE) IN BOLIVIA, J. Lobao Tello mistakenly reports *Caiman latirostris* as being common in the Itonamos, San Pablo, and Manuripi rivers and in the lake at Puerto Suarez. We have examined the specimens he collected from these localities and there are no *C. latirostris* among them. His records apparently are based on misidentified *Paleosuchus*.

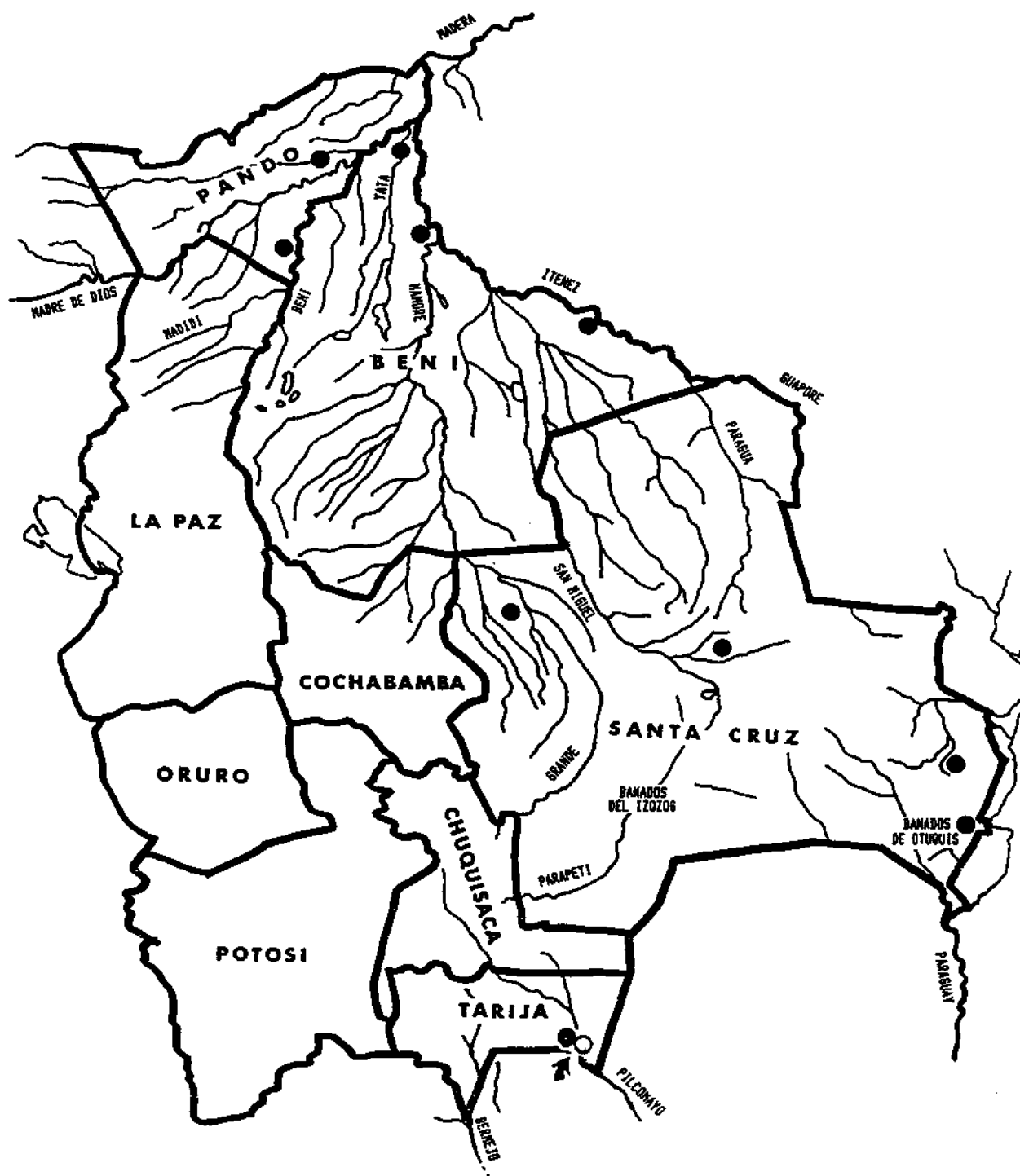


Figure 1. *Caiman latirostris* distribution in Bolivia. The open dot (○) indicated by arrow at bottom of map is the single locality where the species was found in the present survey. Solid dots (●) are localities from Medem's 1973 survey (1983:Map 8).

truly extinct in Bolivia. If that is allowed to happen, Bolivia will have lost a valuable economic resource, its caiman species with the second most valuable hide.

Caiman yacare = Lagarto. This species is found throughout the Bolivian Departments of Beni, Pando, and Santa Cruz, and the lowland portions of Chuquisaca, Cochabamba, La Paz, and Tarija (Fig. 2). It occurs in virtually all permanent water habitats in both the Amazon and Paraguay river drainage basins; rivers, streams, lagoons, oxbow lakes, ponds, swamps, marshes, and even some roadside ditches. It is most plentiful where quiet open waters provide the mature Lagartos with space for courtship and territorial displays, and an abundance of emergent and floating vegetation along the shore provides protective cover for adults and young. The vegetation also provides habitat for insects, snails, frogs, and small fishes which are the prey of young Lagartos, while the open water provides habitat for larger fishes. Medem (1960, 1971) reported similar habitat preferences in Paraguay and Colombia. The species is not abundant in fast water or water that lacks the vegetative cover. This is particularly evident in the large rivers where it is possible to travel for km without seeing the eyeshine of a single Lagarto.

At the present time, the Lagarto is the Bolivian species most heavily hunted for its hide. Over the last decade, it has supported an annual legal export trade of hides from 50,000 to 200,000 Lagartos, and an added illegal trade that brings the total exports to an estimated 400,000 Lagartos a year. As a consequence, though males of the species reach a total length of at least 2.5 m, and females reach 1.8 m, the vast majority of Lagartos encountered are small, usually less than 1.25 m total length.

The breeding season of Lagarto varies from region to region. Information gathered on this survey, indicates that in the region of the upper Itenez river in eastern Santa Cruz, Lagarto court and mate from September to November, build nests and lay eggs in November and December, though occasionally some lay as late as February. However, the survey data also suggest that in the lower reaches of the Beni river in northern Bolivia, Lagarto nest earlier, from August to November. Without fixing any particular region, Medem (1983) states information he received suggests Lagartos nest from the end of August to November, while in the upper Mamore river of central Bolivia, Lovisek (1980) reports Lagarto nest from November to December.

Melanosuchus niger = Caiman. Medem (1983) reports hunting of the Caiman in Bolivia began in 1942. Tens of thousands of hides were exported between then and 1961 when Supreme Decree (= Presidential Decree) No. 05912 established a minimum legal size of 2.1 m in length for Caiman hides and prohibited all hunting of the species from 31 July to 1 January. Despite this Presidential regulation, tens of thousands of additional hides of all sizes, taken throughout the year, have been exported, both legally and illegally. As a consequence of this uncontrolled exploitation, the Caiman is in danger of extinction in Bolivia. The species occurs throughout the lowlands of Bolivia (Fig. 3), but in most localities its numbers have been decimated or it has totally disappeared. While it remains as widely distributed as it was during Medem's 1973 survey, the present survey teams did not encounter *Melanosuchus* nearly as often as Medem did. Only in a very few localities, mostly quiet water habitats, is it sufficiently abundant to enable the survey teams to encounter more than one or two specimens, usually juveniles or subadults, in a night. Hunters are still finding a few relatively untouched populations in remote areas -- in August 1986, 927 salted and dried Caiman hides were seized by CDF guards on the Rio Apere northwest of Trinidad, Beni, after the single-engine airplane carrying the contraband hides crashed and was abandoned by its operators; and in May 1987, one dealer in Beni was alleged to have 8,400 Caiman hides ready for shipment to illegal buyers in Paraguay. Such occurrences are becoming less frequent as the species continues to slip toward extinction. The Caiman is the second most endangered crocodilian in Bolivia, and will follow the Overo, *C. latirostris*, to commercial extinction and then to actual extinction if existing conservation laws and regulations are not enforced soon.

Hunters and tanners were questioned to determine what size Caimans attained in the past. The largest hide measured by a tanner in Trinidad was 5.25 m, while one in Cochabamba reported years ago having received one hide in excess of 7 m long. Most agreed that any Caiman over 4 m total length was



Figure 2. *Caiman yacare* distribution in Bolivia. Enclosed stars (★) are localities where the species was found during the present survey. Solid dots (●) are localities from Medem's 1973 survey (1983:Map 8).

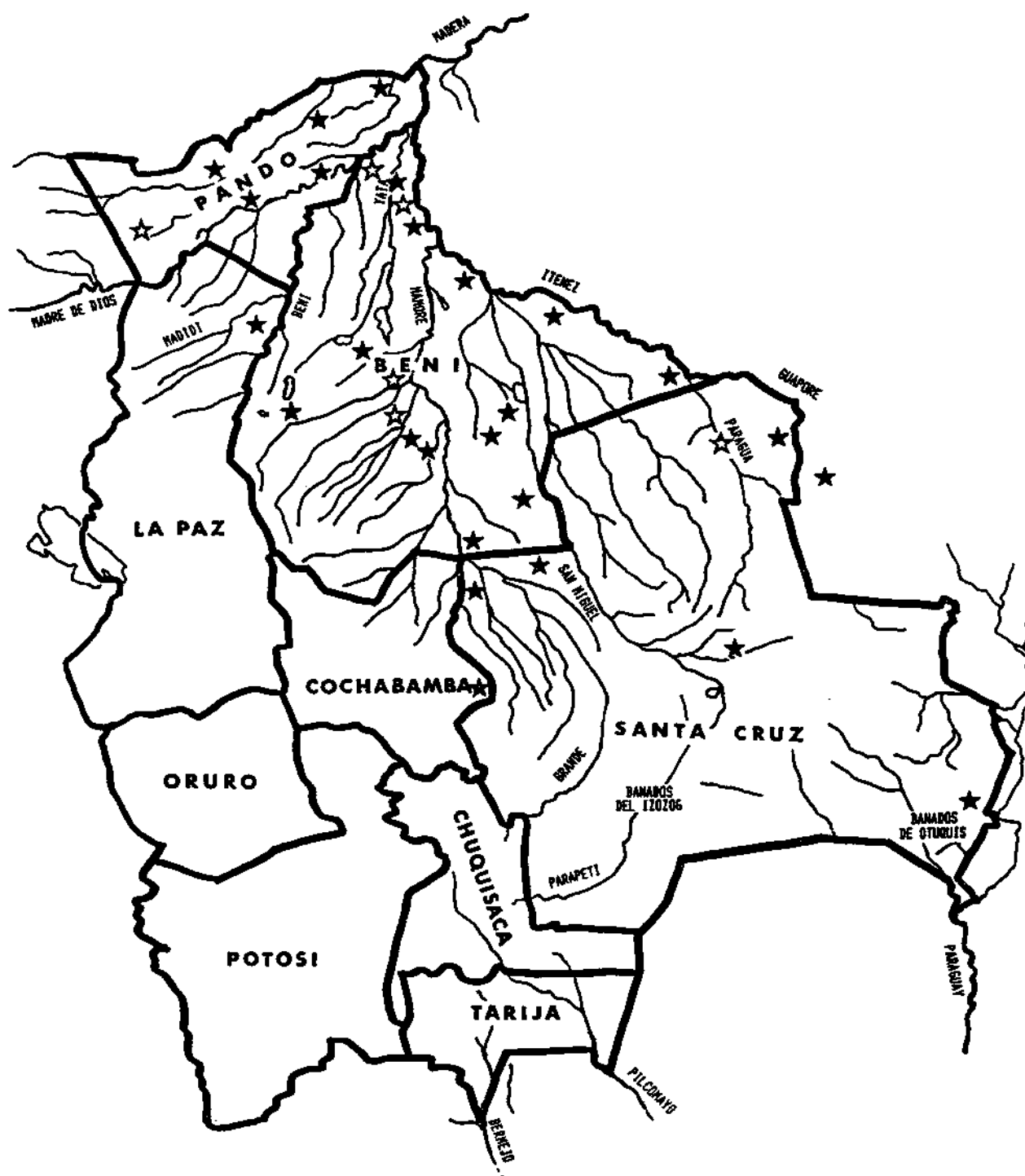


Figure 3. *Melanosuchus niger* distribution in Bolivia. Open stars (☆) are localities where the species was found during the present survey. Solid stars (★) are localities from Medem's 1973 survey (1983:Map 8).

unusually large. Today, any Caiman over 2 m total length is "big," and ones approaching 3 m are virtually non-existent.

Today, the Caiman occupies much the same habitat as the Lagarto, *C. yacare*, rivers, streams, lagoons, and oxbow lakes, that have a well-vegetated shoreline. They tend to be most frequent in situations which provide an expanse of quiet, open water in addition to the vegetative cover. Data produced by the survey do not clarify whether or not Caiman and Lagarto occupied somewhat different habitats prior to their decimation by hide-hunters.

Caimans call year-round, but are more vocal during mating season. In eastern Santa Cruz, mating takes place from September to November. Nesting occurs shortly after mating, and nests can be found from December through January.

Paleosuchus palpebrosus = Cocodrilo, and *Paleosuchus trigonatus* = Cocodrilo and Caiman negro. These two species are discussed together, because the two are confused by hunters and laymen alike, because their habitats and other aspects of their ecology in Bolivia are similar, and because neither is heavily hunted.

Both species of Cocodrilo occur widely through northern Bolivia, but only *P. palpebrosus* is found in central and southeastern Bolivia (Figs. 4 and 5). However, their distributions are disjunct and not continuous. They are found in large rivers and small streams (see Vanzolini and Gomes 1979:206-208). They are found at night along the stretches of shore that are devoid of floating and emergent vegetation. They sit exposed on bare sand, gravel, or mud banks, or shelter themselves behind piles of dead tree trunks and limbs. Not one was found among the living plant cover. So consistent was this choice of microhabitat, that as soon as it was possible to determine if a particular eyeshine emanated from a patch of green vegetation or from a bare bank, we could predict whether or not it was *Paleosuchus* or *Caiman*.

Both species of Cocodrilo possess large osteoderms in their belly scales. This heavy dermal armour makes the hides essentially worthless as leather. Hide dealers in Bolivia do not buy the hides, so normally hunters do not kill them. A very few are killed by mistake, but there is no concerted hunting pressure on these species. As a consequence, all available data suggest their populations and distributions are undiminished, except near cities where they have lost habitat to urban sprawl.

Habitat Distribution: Nearly two-thirds of Bolivia lies in lowlands occupied by tropical, subtropical, and temperate forests and savannas (Fig. 6). While the present survey, and the 1973 survey by Medem (1983), demonstrated that caimans occur throughout the lowlands, the greatest numbers occur in the habitats of the Beni Plain that stretches from Puerto Heath and the Madre de Dios river of northern La Paz Department to the Huanchaca and Negro highlands of eastern Santa Cruz Department (Fig. 7). The Beni Plain's 100,000 km² of savannas and 171,131 km² of forests make up 25% of Bolivia's area.

Prior to being hunted for their hides, Bolivia's caimans probably lived in every permanent watersource in the lowlands, and temporarily occupied other habitats during the wet season. Eliana Flores (1986) conservatively estimates that permanent water habitats, lakes, rivers, and streams, occupy 5,812 km² of the Bolivian lowlands, but provides no estimate of seasonally flooded habitats. During the present survey, more than 700 km of aerial transects were flown in the Department of Beni, in an attempt to provide an independent estimate of wetland habitats. For purposes of the transects, all habitats were grouped into:

- C = curichi (a small, permanent water lagoon, with extensive vegetation, usually an oxbow lake formed when the river changed channels)
- F = hardwood forest (other than gallery forest), usually rain forest
- G = gallery forest bordering a river or stream
- L = lagoon or lake with a large expanse of open water (permanent water)
- P = palm savanna

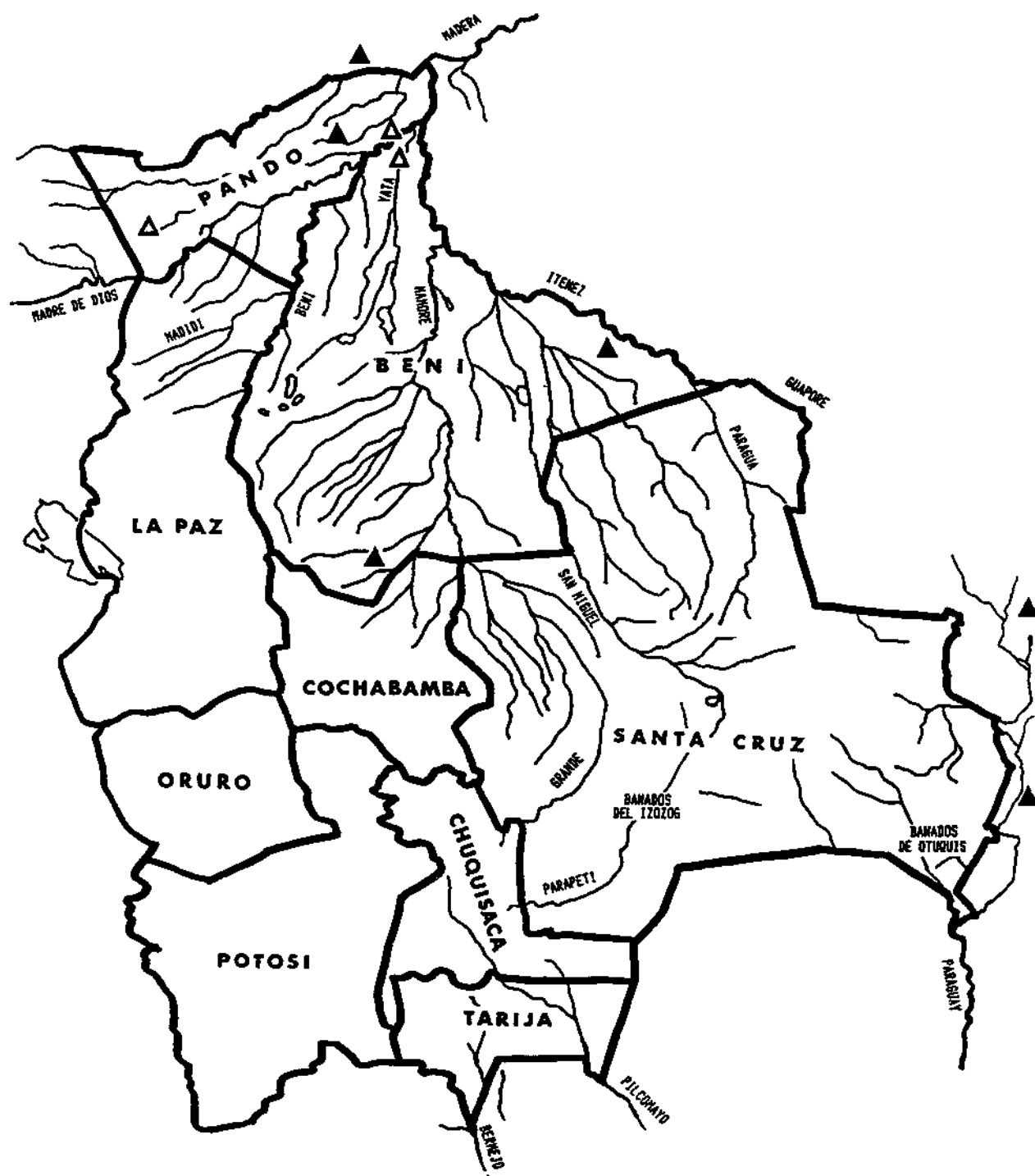


Figure 4. *Paleosuchus palpebrosus* distribution in Bolivia. Open triangles (\triangle) are localities where the species was found during the present survey. Solid triangles (\blacktriangle) are localities from Medem's 1973 survey (1983:Map 8).

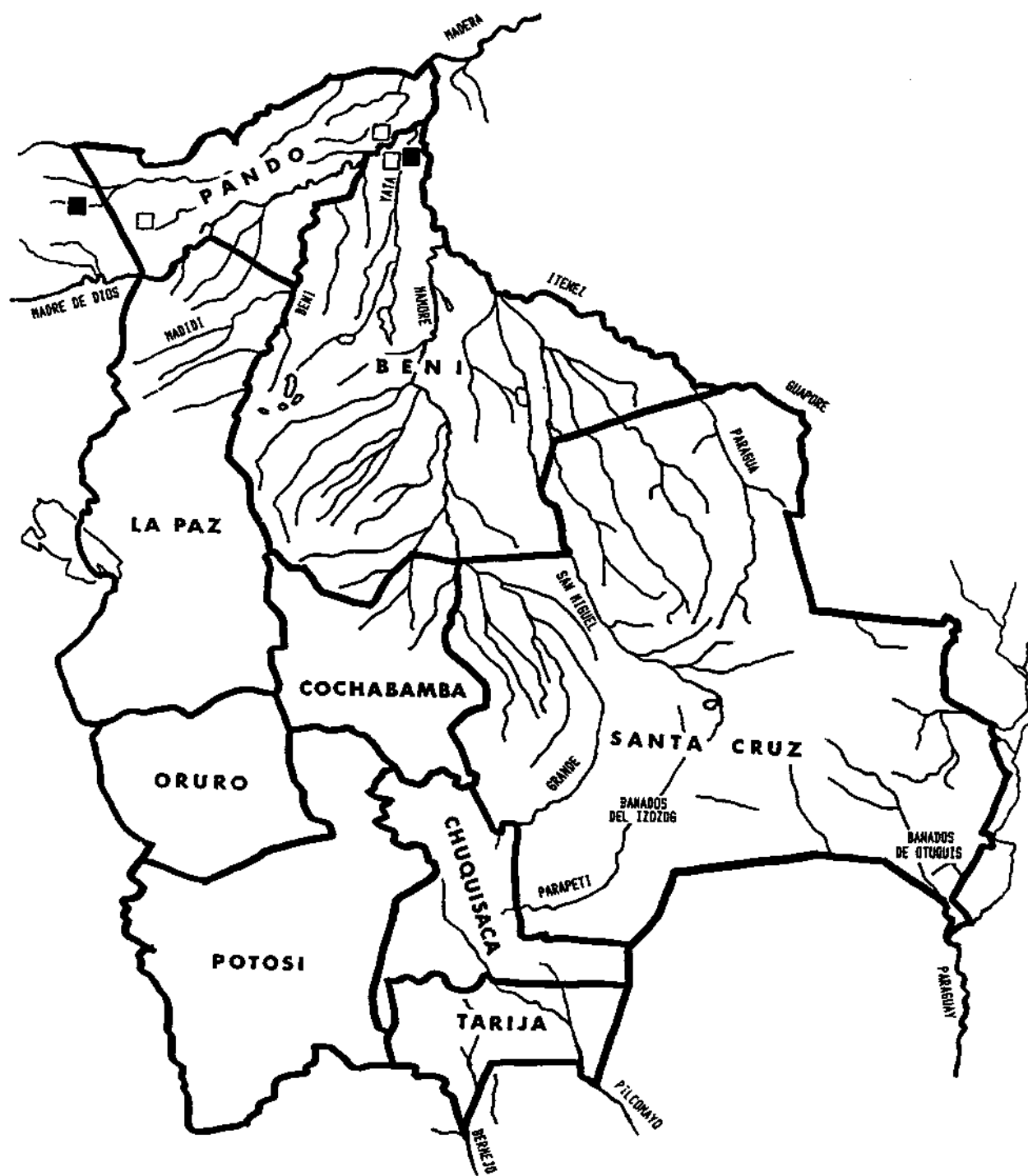


Figure 5. *Paleosuchus trigonatus* distribution in Bolivia. Open squares (□) are localities where the species was found during the present survey. Solid squares (■) are localities from Medem's 1973 survey (1983:Map 8).

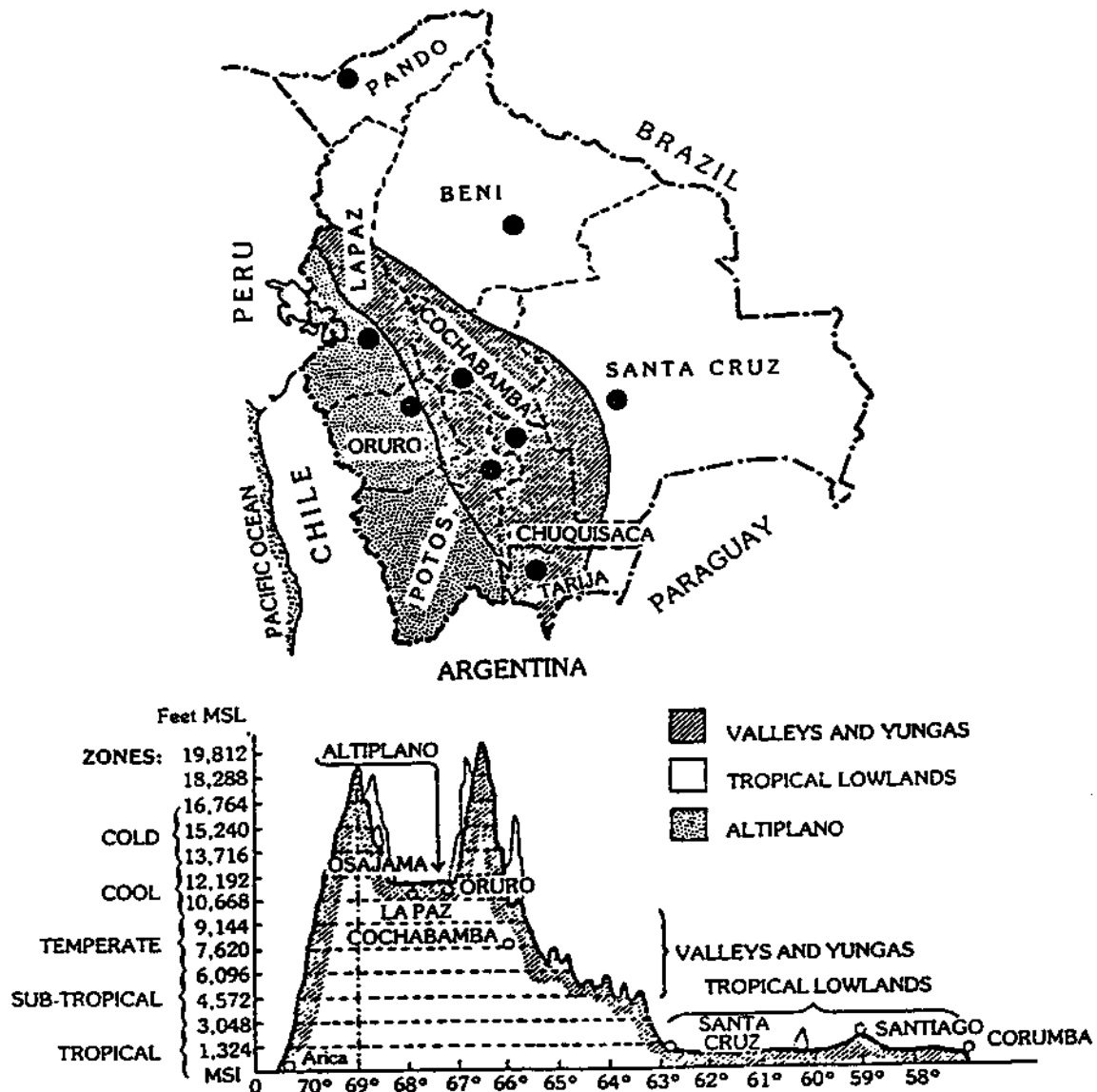
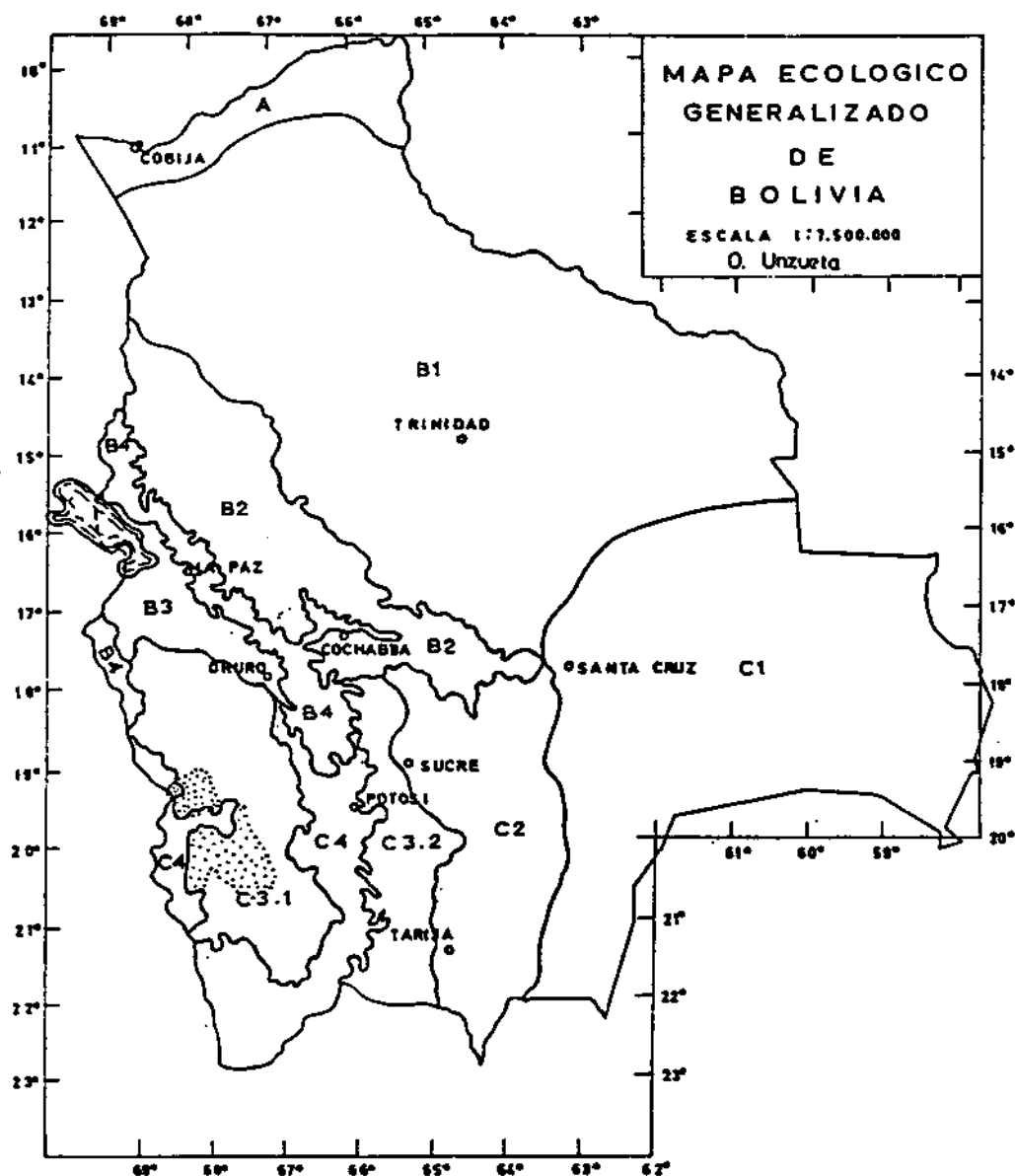


Figure 6. Geographic profile of Bolivia (from Freeman, Cross, Flannery, Harcharik, Hartshorn, Simmonds, and Williams 1980:1-3). Caimans are confined to Bolivia's tropical and subtropical lowlands.



REFERENCE KEY

- | | |
|------------------------------|----------------------------|
| A. Tropical Region | B4. Subtropical Andes |
| A. Tropical lowlands | C. Temperate Region |
| B. Subtropical Region | C1. Temperate lowlands |
| B1. Subtropical lowlands | C2. Temperate valley lands |
| B2. Subtropical valley lands | C3. Temperate highlands |
| B3. Subtropical highlands | C4. Temperate Andes |

Figure 7. Generalized ecological zones of Bolivia (adapted from Unzueta 1975). In Bolivia, the greatest numbers of caimans are found in the wetlands of the Beni Plain, B1.

- Pt = pantano or marsh, usually *Cyperus* marsh (permanent water)
 R = river (permanent water)
 Sw = wet savanna, seasonally flooded (seasonal habitat)
 Sd = dry savanna
 Strm = streams (usually permanent water)

These transects were not randomly selected, but rather were flown between Trinidad, Santa Ana, Reyes, and Versalles (Fig. 8) in route to collecting localities. None of the transects crossed the lake region of northcentral Beni. In addition, unless sunlight reflecting off the water could be seen through the leafcover, closed canopy forest obscured the presence of small streams. As a consequence, while the transects are broadly reflective of the relative abundance of habitat types, they undoubtedly under estimate year-round wetland habitats in the Beni and should not be treated as a statistically rigorous sample.

The transects suggest that permanent wetland habitats, year-round habitat for caimans, occupies approximately 23%, or 62,360 km², of the area of the Beni Plain (Fig. 9). Seasonally wet habitat occupies an additional 27%, or 73,205 km². These proportions are not typical of the drier areas of the Bolivian lowlands in Pando, Santa Cruz, Chuquisaca, and Tarija. If it were, the entire 659,149 km² of Beni, Pando, northern La Paz, and Santa Cruz, the 60% of Bolivia occupied by the Amazon basin (Flores 1986), could provide a total of 151,604 km² of year-round habitat for Bolivia's five species of caiman.

Not all the permanent wetlands are utilized equally by the caimans. As indicated above, *C. latirostris*, *C. yacare*, and *Melanosuchus* are most frequently encountered in habitats that provide both open expanses of quiet water and vegetative cover near shore; the two species of *Paleosuchus* are most frequent in rivers and streams where the banks are bare and cover is provided by dead logs and brush piles. Much of the flat Beni Plain fills with water during the November to May rainy season; savannas flood and rivers rise 3 or 4 m. The elevation at Trinidad is approximately 160 m, and at Riberalta, 440 km further north (downstream in the Amazon Basin), the elevation is still about 145 m. The falling river levels expose great expanses of mud and sand, leaving the Overos, Lagartos, and Caiman with little or no cover in which to hide. This has to be one of the reasons that all species of caimans are scarce in the large rivers. A second reason is the rivers are easily hunted. Hunters told the survey teams that the major rivers essentially have been hunted out for more than a decade.

The extent of available permanent habitat, coupled with a small breeding size and rapid attainment of sexual maturity, is undoubtedly what has allowed Bolivia's Lagarto population to sustain the level of exploitation to which it has been subjected. That same intensive level of exploitation, directed at the larger and more slowly maturing Caiman and Overo, has resulted in their endangerment.

The seasonally flooded habitats allow caimans, particularly the Lagarto, to move from one drainage system to another and to colonize all suitable permanent water habitats. The headwaters of many of Bolivia's rivers are only separated from other rivers or from lakes by short distances of seasonally flooded habitat. For example, the headwaters of the Ipurupuru river, a tributary of the Machupo river flowing into the Itenez, is separated from the middle Mamore river by about 2 km of seasonally wet savanna and scattered curichis (vegetated oxbow lakes).

Similarly the Negro river, a tributary of the Beni river, is separated from the Benicito, a tributary of the Yata river, by seasonally flooded habitat. The same is true of the San Martin river and the Paragua river; and even the Guapore river, a tributary of the Amazon, and several tributaries of the Paraguay river. Numerous other examples could be cited.

Population Densities: Of the three commercially exploited species, *Melanosuchus*, *C. latirostris*, and *C. yacare*, only the latter species, the Lagarto, was encountered sufficiently often to allow any estimate of population densities.

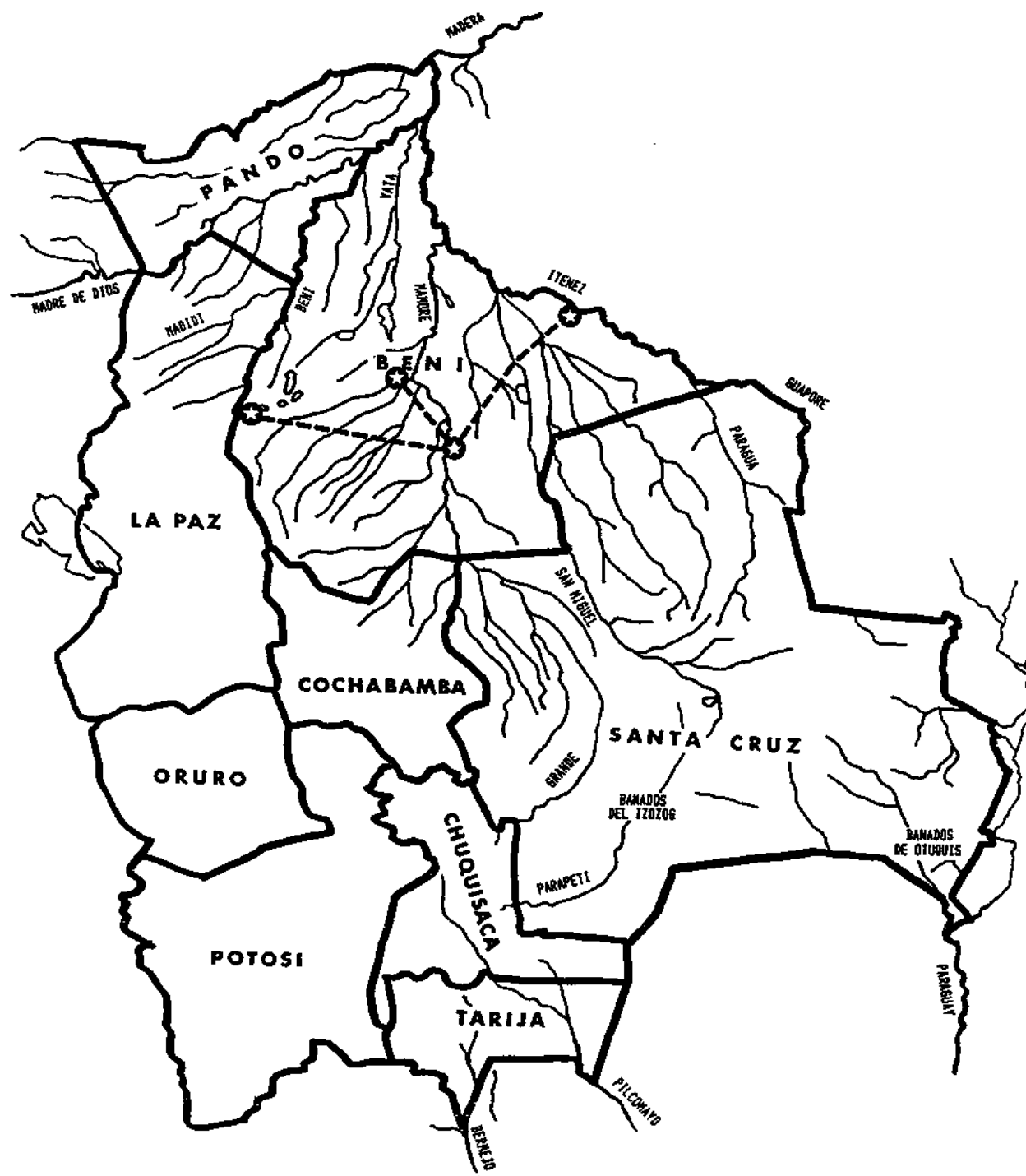


Figure 8. Aerial transects of habitats in the Beni. The transect routes radiate out from Trinidad; northeast to Versalles on the Itenez River; northwest to Santa Ana on the Yacuma River, near its confluence with the Mamore River; and west to Reyes, near the Beni River.

The following estimated densities of Lagartos, *C. yacare*, were encountered during the present survey.

Lagarto, *C. yacare*, are not endangered in Bolivia, but there is ample evidence that the resource is suffering severely from lack of conservation management.

The Lagarto were more abundant in quiet water embayments and lakes (lagos, lagunas, curichis, and arroyos) with vegetative cover, and were relatively scarce in moving water situations that lack cover. However, nowhere in Bolivia, in any type of habitat, did the survey teams encounter populations of Lagartos as dense as they are in parts of the Brazilian pantanal, or as dense as *C. crocodilus* populations are in Venezuela.

Coastal Venezuelan populations of *C. c. crocodilus* reach densities of 0.2-196.6 per km of shore (Seijas 1986). In inland riverine habitats in Venezuela, densities of 2.52 per km are found, with a range of 0.7 to 150.0 per km, and in quiet lagoons an average density of 23.4 per km occurs, with a range of 8.0 to 45.5 per km (Gorzula and Paolillo 1986). In addition, large adults over 1.5 m total length account for between 14% and 29% of the Venezuelan populations (Staton and Dixon 1975, Ayarzagüena 1983, Seijas 1984, Woodward and David 1985), while large adults comprise no more than about 3% or 4% of the populations seen by the Bolivian survey teams. *C. yacare* reach similar densities in protected habitats in the Brazilian pantanal (pers. comm. from P. Brazaitis, NYZS, and P. Crawshaw, IBDF), but where they are intensively hunted in Brazil, *C. c. crocodilus* populations consist largely of animals less than breeding size (Magnusson 1980, 1982).

In the rivers of Peru, *C. crocodilus* populations have densities of from 0.68 to 9.0 per km, and adults over 1.25 m account for 3% of the total (Moya et al. 1980; Vasquez 1981).

The difference between Bolivia and Venezuela and Brazil is not in the biology of the animals. It reflects the total lack of conservation management of the caiman resource in Bolivia (see Resource Utilization, and Wildlife Laws below) -- not a single species of wildlife is professionally managed in Bolivia.

Everywhere the survey teams went in Bolivia, wildlife officials, caiman hunters, ranchers, and local citizens told them about some lagoon, curichi, or river which reputedly was swarming with Lagarto. The teams visited a number of these celebrated localities, either alone or in the company of the person who originally claimed there was a glut of Lagarto at that site. Not one of these localities contained a large, dense population, and not one supported a high percentage of large adult animals. The discovery that the population was not as large as believed always surprised the person who originally told us about it, and it inevitably prompted him to regale us with a story about yet another location with a mythical horde of Lagartos. This was not a deliberate effort to mislead the team members. Rather it resulted from the widespread public misconception that Bolivia's wildlife is endlessly abundant. That city dwellers might believe this is not surprising, but it is distressing to find hunters, ranchers, and especially wildlife officials who are so naive.

Resource Utilization: While large caimans of all five species were encountered during the present survey, the vast majority of populations consisted of juveniles and subadults. This is the direct result of Bolivia's poor management of the caiman resource and lack of enforcement of existing wildlife laws. As noted seven years ago by Freeman et al. (1980), illegal hunting for animal skins and the ease of circumventing laws are threatening the future existence of Bolivia's wildlife and parks and is a direct result of the failure of the Centro de Desarrollo Forestal (CDF) to implement conservation legislation and programs. Wildlife, both plant and animal, is viewed solely in terms of how much money it will yield through short-term exploitation (Freeman et al. 1980) and not through management for a sustained utilization. These problems cannot be overcome until a professional cadre of wildlife and park planners, managers, and administrators is created within CDF (Freeman et al. 1980).

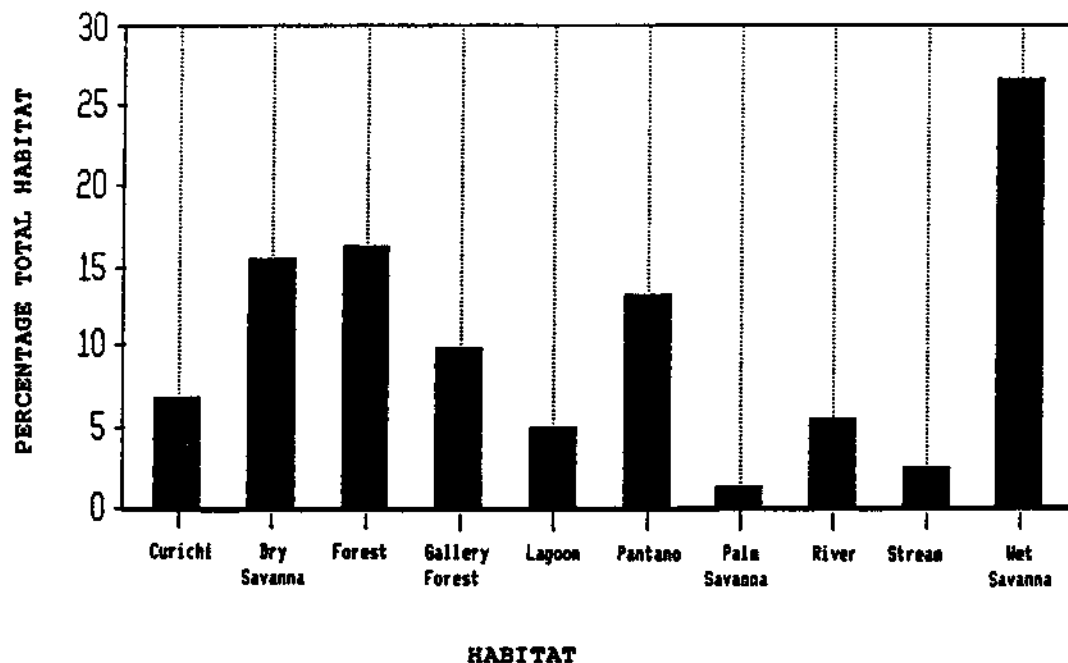


Figure 9. Habitat frequency expressed as a percentage of total time flown in aerial transects. Curichi, lagoon, pantano, river, and streams are permanent water habitats. Wet savanna, and some forest, gallery forest, and palm savanna are seasonally flooded.

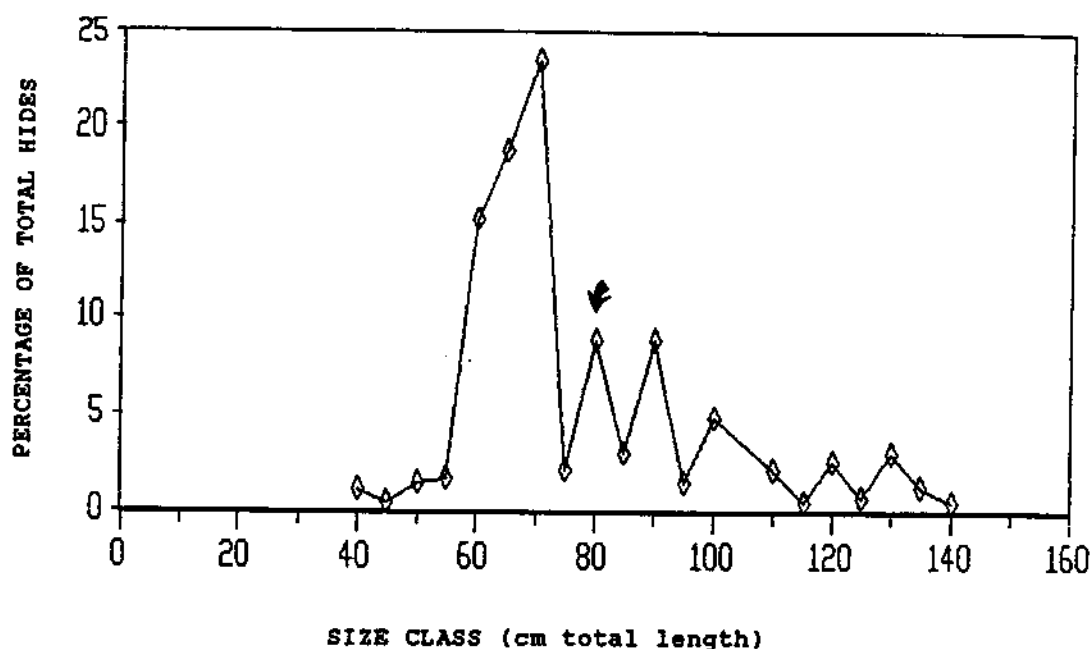


Figure 10. Size classes of Lagarto, *Caiman yacare*, flanks harvested legally in 1985 and 1986 as represented by a sample of 16,000 fully tanned, dyed, and glazed hides in the warehouses of the six tanneries of the Asociación de Industriales de Cueros de Saurios. A flank consists of the soft strip of hide starting immediately under the chin and extending along the neck, over the front leg, alongside the trunk between the bony dorsal (back) and ventral (belly) scales, under the hindleg, and ending just behind the cloacal vent. It is the hide most frequently flayed from the Lagarto, accounting for more than two-thirds of all crocodilian hides entering international trade each year. The arrow indicates the size flank produced by a 1.5 m Lagarto, the minimum size allowed under Bolivian law.

Hard biological data on Bolivian *C. yacare* are not available, but data on *C. crocodilus* suggest that female Lagarto should reach sexual maturity at about 1.3 m total length and an age of 4 years (Staton and Dixon 1977, Magnusson 1982). Most adult female Lagartos are around 1.4 to 1.5 m, and a maximum total length is about 1.77 m (Medem 1983). Males, if not killed, will grow to more than 2.0 m total length, and some will exceed more than 2.5 m. Lagarto can be managed for a sustained harvest, by protecting the breeding females. Without that protection, females will be lost, production of eggs and young will decline, and there will be little recruitment into the adult population to replace the animals killed for their hides. Since there is such a size difference between sexually mature females and males, limiting the hunt solely to Lagartos more than 1.5 m total length results in harvesting mostly males.

In 1961, Supreme Decree No. 05912 prohibited the hunting of Lagartos less than 1.5 m in total length. In 1962, Supreme Decree No. 05987, reaffirmed that minimum size and also closed the hunting season from 1 May to 1 October. Even though similar minimum sizes and closed seasons have been reaffirmed repeatedly by Supreme Decree No. 08063 of 1967 (the closed season was shifted to 1 July-31 December) and numerous Ministerial Resolutions since then, there is virtually no enforcement of the size limit or closed season. Hunting takes place opportunistically throughout the year. As a consequence, the breeding population has been decimated. Most Lagarto have been eliminated from the easily accessible large rivers, and large populations, even of small Lagarto, are found only in the more inaccessible oxbow lakes and marshy lagoons. The species survives because a few females manage to reach sexual maturity, to breed, to produce eggs, and to contribute to the next generation before being killed for their hides. That this has happened is evident not only in the age/size structure and density of the wild populations, but also in the size of animals being killed for their hides.

The inventory of finished Lagarto hides (i.e., hides that have been tanned, dyed, and glazed) in the warehouses of the six tanneries of the Asociación de Industriales de Cueros de Saurios (ASICUSA), provided data on the sizes of Lagarto hides harvested in Bolivia with permission of CDF officials (Fig. 10). Each tannery supplied the inventory team with a detailed list of the sizes and numbers of hides it had in storage. To confirm the accuracy of the list, the team, without prior consultation with the tannery personnel, selected, counted, and measured approximately 16,000 Lagarto flanks, 7% of the total hides. The counts and measurements were then checked against the company's records to uncover any discrepancies.

A 1.5 m Lagarto, the minimum legal size under Bolivian law, yields a flank approximately 80 cm in length. Nearly two-thirds of the Lagarto hides, 65%, are less than legal size (Fig. 10). The smallest flanks measured only 40 cm, the equivalent of 72 cm Lagarto. This is strong evidence that the resource has been grossly mismanaged. Allowing the harvest of such small-sized Lagartos assures that the breeding females are destroyed and that the reproductive potential of the wild populations will continue to decline.

At the present time, *C. yacare* is not an endangered species in Bolivia. The species still occurs throughout the country in every suitable habitat. The killing of under-sized Lagarto has severely damaged the resource by all but eliminating the breeding adults. However, the widespread presence of juveniles indicates successful nesting is occurring. In addition, 35% of the inventoried hides were from Lagartos larger than 1.5 m, and the largest flanks were 140 cm in length, the equivalent of a 2.5 m Lagarto. Clearly, if existing laws governing the killing of Lagarto were enforced, there are sufficient numbers of large animals to rebuild the breeding population within a few years. Conversely, if laws are not enforced and if progressively smaller sizes are killed for their hides, the Lagarto will become endangered.

Lack of active conservation management not only has hurt the Lagarto, *C. yacare*, it has endangered the Caiman, *M. niger*. Supreme Decree No. 05912 of 1961 prohibited the killing of Caiman, *M. niger*, less than 2.1 m in total length and set a closed season between 31 July and 1 January. That size limit and closed season (adjusted to 1 July-31 December) has been reaffirmed in numerous laws and regulations to the present time. Nevertheless, Caiman of all sizes are killed throughout the year. Since the Caiman reaches sexual maturity at between 2.0 m and 2.4 m (Medem 1963, Magnusson 1982) and an age of about 5 years, but they are killed at a much smaller size, the majority of Caiman are killed before they can contribute to

the next generation. With the breeding adults gone, the *M. niger* populations have crashed and the species is in danger of extinction in Bolivia.

M. niger is on Appendix I of CITES so international commercial trade is prohibited. Enforcement of this prohibition would alleviate the pressure on this species and allow its populations to recover. In addition, if the harvest of Lagarto, *C. yacare*, were limited to large hides as required by Bolivian law, it would ease enforcement. CDF staff would only have to check the purchases and holdings of a few dozen hide buyers and the six tanneries, not every hunter in the field. Commercial hunters do not hunt for sport. They hunt for money. If they cannot sell the hides they produce, they will not spend the money and time killing Caiman or undersized Lagarto.

Bolivian Wildlife Law: In Bolivia, wildlife conservation problems result as much from official non-feasance as it does from non-compliance by the legal hide industry.

Unlike poachers and smugglers, the ASICUSA members operate openly - - their hides are checked by CDF officials between the purchase from the hunter and arrival at the tannery. After tanning, Bolivia law requires that they be checked again in Cochabamba before export. While a majority of ASICUSA's present holdings of Lagarto hides are under the legal size limit, these hides, most of which were acquired in 1985, have been validated by CDF. Nevertheless, the ASICUSA tanners recognize that their future depends on better management of the Lagarto resource. To that end, they have pledged not only to abide by all wildlife laws, but voluntarily to put into practice new procedures that will assist the Parties to CITES, the CITES Secretariat, and CDF in implementing the Convention in Bolivia. To do this, the ASICUSA members must be allowed to operate legally.

The inventory disclosed that ASICUSA has on hand the finished hides of more than 109,000 Lagartos. These hides were purchased and tanned, in part, under the 1985 export quota of 100,000 established by cooperative agreement between CDF and CITES, and in part, under the 1986 export quota of 50,000 established by the President of the Republic of Bolivia under Supreme Decree No. 21312. Yet, in 1986 and 1987, three separate national directors of CDF illegally sold Bolivia/CITES country of origin export permits in the amount of the annual quotas to hide exporters in Paraguay. Since the illegal permits were for the total amounts of the quotas, no additional permits could be issued, thereby denying ASICUSA tanners the opportunity of exporting their legal hides to international markets. Several of the ASICUSA members have more than U.S. \$1,000,000 invested in 1985 and 1986 hides. Unless they are allowed to recoup their investment by selling these legal hides on the international market, they will go out of business. However, the illegal sale of CITES permits to Paraguay companies had an effect far beyond its immediate economic impact on ASICUSA. By providing a ready outlet for poached hides, the illegal sale of the permits more than doubled the number of Lagartos killed, and it sanctioned and encouraged the transnational movement of illegal wildlife products in violation of CITES.

Bolivian Supreme Decree No. 05912 of 27 October 1961, that set minimum size limits and a season on the hunting of Lagarto and Caiman, also prohibited the export of raw hides of these two species, and allowed only the export of crusted (= semi-tanned) and finished (= fully tanned, dyed, and glazed) hides. Secretarial Regulation No. 133225 of 29 March 1966 prohibited the export not only of raw hides but also of crusted hides, thereby only allowing exports of fully tanned hides, and only by licensed tanners. Ministerial Resolution No. 279/72 of 10 May 1972, continued the prohibition of exportation of any but finished Lagarto and Caiman hides, as did Ministerial Resolution No. 14316-74 of 14 May 1974. Other resolutions fixed a tax on every Lagarto and Caiman hide tanned and exported. Still later resolutions allow the finished hides to be exported solely by members of ASICUSA. It should be noted that, with few exceptions, Bolivian general law prohibits monopolies. One of only two or three exceptions involves wildlife, so outlawing all exports of fully tanned, dyed, and glazed caiman hides except by ASICUSA members is entirely legal and is designed to stimulate conservation and development by assuring that legitimate tanners provide the sole market for legal hides and in turn make the only exports. This was most recently reaffirmed in Supreme Decree No. 21312 of 27 June 1987, which prohibited all wildlife exports for a period of three years, except for an annual export of 50,000 Lagarto hides by members of ASICUSA.

When ASICUSA members are not allowed to export their legal hides, it not only violates Bolivian laws, it also puts ASICUSA at an economic disadvantage since the illegal operators do not pay the cost of tanning, dyeing, and glazing their hides, and do not pay taxes on those hides. Faced with this sanctioned illegal trade, it is little wonder that the members of ASICUSA have traded in undersized hides. Any hides not bought by ASICUSA are bought by illegal dealers and shipped to Paraguay.

These problems were recognized in the Resolution contained in Conf. 5.2 from the 5th Meeting of the Conference of the Parties in Buenos Aires, Argentina, 22 April to 3 May 1985, which states that "...other countries are taking advantage of the economic and financial weaknesses of the Bolivian authorities in encouraging... illegal trade..." However correct its intent, Conf. 5.2 did not correct the problem. As mentioned above, ASICUSA members have not been able to export legal hides since 1986, because three former national Directors of CDF sold to illegal dealers in Paraguay sufficient Bolivian/CITES country of origin export permits to cover the entire 1985 and 1986 quotas for the annual export of Lagarto hides. Because of this continued sanctioning of illegal wildlife trade, in October 1986, the Standing Committee of CITES recommended that the Parties to the Convention no longer accept Bolivian export permits.

While this action by the Standing Committee is understandable, its main affect was to penalize ASICUSA, the only legal tanners and exporters of Lagarto hides, and leave the illegal buyers with a corner on the caiman resources. Prior to the October 1986 decision of the Standing Committee, Supreme Decree No. 21312 of 27 June 1987, had prohibited all wildlife exports for three years, except for the export of 50,000 Lagarto hides by the members of ASICUSA. The action of the Standing Committee cut off the only legal method ASICUSA members had to recover their investments in 1985 and 1986 hides and left the trade in the hands of illegal buyers.

The illegal trade in Bolivian Lagarto hides actually increased in volume following the 1985 CITES Conference in Buenos Aires, and seems to have increased yet again after the CITES Standing Committee recommended closing down all Bolivian exports. Today, without export permits of any kind, Bolivian *C. yacare* hides and *M. niger* hides are being flown aboard small airplanes to Paraguay, where they are exported to Europe and Asia, primarily France, Italy, and Japan. Almost any day of the week, radio conversations between hunters on outlying ranches and illegal buyers in Trinidad and other towns in the Beni can be heard discussing the current price of hides being paid in Asuncion. Reports received from the field on 1 July 1987 indicate that poaching of Lagarto and Caiman is at an all time high in southwestern Brazil, despite commercial hunting having been outlawed in Brazil in 1967 when Lei No. 5197 came into force. The rampant illegal hunting is the direct result of illegal hide buyers operating in Bolivia and Paraguay. The need for conserving caimans has reached crisis level in southern South America.

The operating principle behind CITES is international cooperation so that importing nations do not provide markets for wildlife exported illegally from its country of origin. Without that cooperation, no nation can protect and properly manage a wildlife resource as valuable as wild crocodilians. In the case of Bolivia, CITES failed to uphold that principle.

Recognizing the role played by CDF officials in the illegal wildlife trade in southern South America, the Parties to CITES passed Resolution Conf. 5.2 on Implementation of the Convention in Bolivia, which required a 50% reduction in Bolivia's wildlife exports (see also Doc. 6.20.C from the 6th (Ottawa) Meeting of the Conference of the Parties to CITES). When the sale of Bolivia country of origin CITES permits continued to be sold to a company in Paraguay, the Standing Committee recommended closure of all imports from Bolivia, and alerted the Parties by Notification No. 413 of 28 November 1986. However correct that closure might be, it failed to act against the primary source of the illegal trade, Paraguay, the immediate buyer and transshipping nation, and France, Italy, and Japan, the ultimate market and destination. Bolivia played a supportive role in the illegal trade by supplying the CITES permits that allowed companies in Paraguay to ship illegal hides from Paraguay to buyers in Europe and Asia. By failing to implement the Convention, Paraguay played an active role in illegal wildlife trade, not only out of Bolivia, but also out of Brazil and other nations in Latin America. CITES must do more to stop the illegal

trade into and out of Paraguay, than simply urging Bolivia's, "...neighboring countries to co-operate to the maximum of their ability in the control of the illegal trade across their borders..." [Resolution Conf. 5.2]

In addition, France, Italy, and Japan must start proper implementation of CITES by no longer allowing importation of illegal wildlife exports from Paraguay and other illicit shipping points. By Decree No. 18.796 of 1975, Paraguay banned all commercial hunting and export of native mammals, birds, reptiles, and amphibians. CITES Notification No. 225 of 13 October 1982 informed all the Parties to CITES that Paraguay Presidential Decree No. 18.796 allows the import of wildlife products for manufacture and re-export, and CITES Notification 388 of 7 May 1986 advised that Decree No. 13806 of 17 February 1986 specifically allows the export of shoes made from *Boa constrictor* and *Eunectes* skins. However, the importation and re-exportation of other CITES listed species, including all crocodilians, would require CITES export permits from the country of origin and CITES re-export permits from Paraguay. CITES Notification No. 225 of 13 October 1982 made it clear that Paraguay officials have not issued CITES export permits or re-export permits for commercial purposes since 29 July 1982. Therefore, CITES officials in France, Italy, and Japan knew that shipments of raw or crusted lagarto hides (not manufactured items) covered by Bolivia country of origin permits and shipped from Paraguay (without CITES re-export permits from Paraguay) were illegal. Yet, each of these nations allowed the importation of such shipments during the past 2 years.

The Parties to CITES need to take sanctions against Paraguay, France, Italy, and Japan until those nations effectively implement the Convention.²

In an extraordinary demonstration of his determination to break the pattern of illegal activities that has hindered implementation of CITES in Bolivia, Víctor Paz Estenssoro, the President of the Republic of Bolivia, agreed that the CITES Secretariat could place an expatriate expert in CDF for a period of two years to oversee all CITES operations (see CITES Doc. 6.20). That expatriate specialist will develop and implement new procedures for regulating wildlife exports and will train a cadre of administrative and enforcement personnel to operate the program. Though the present administration of CDF has pledged support for the program, and the entire operation will be under the administrative control of the national Director of CDF, should any problem arise, the specialist will be able to speak directly to the President. This individual is expected to begin work in late 1987. Once this specialist is in place, implementation of the Convention in Bolivia should occur rapidly. Few other sovereign nations have so dramatically demonstrated a willingness to comply with the requirements of the Convention by accepting an expatriate to oversee its CITES operations.

However, Bolivia cannot properly implement the Convention as long as actions by the Parties and the Standing Committee discourage legal trade from Bolivia and favor illegal trade by companies operating in Paraguay. Until the ASICUSA tanners can legally export their hides under CITES, they cannot provide a market in Bolivia for legal hides from professionally managed conservation programs. The Parties to CITES must recognize Bolivia's CITES export permits when, and only when, they cover shipments of fully tanned, dyed, and glazed *C. yacare* hides from ASICUSA tanners.

ASICUSA members have cooperated fully with the CITES survey teams in developing a series of procedures that should assist the Parties to CITES in identifying legal exports from Bolivia and illegal exports from neighboring nations. These procedures are described in the resolution appended to the end of this report, a resolution offered for discussion and possible approval by the Parties at the 6th Meeting of the Conference of the Parties in Ottawa, Canada, 12 to 24 July 1987.³

² This was debated at length at the 6th Meeting of the Conference of the Parties to CITES in Ottawa, Canada, 12-24 July 1987, and resulted in Resolution Doc. 6.19.1 which urged all Parties to strengthen their efforts to control shipments of CITES-listed species.

³ Most of the concerns covered by this draft resolution were included in Resolution Doc. 6.20.1, prepared and submitted by the countries of the Latin American and Caribbean region, and approved at the 6th Meeting of the Conference of the Parties to CITES in Ottawa, Canada, 12-24 July 1987.

ACKNOWLEDGEMENTS

Particular thanks are extended to Professor Fred G. Thompson (Florida State Museum, Gainesville, Florida, U.S.A.), who led one of the survey teams from June to September; Carlos Alvarez (CDF Santa Cruz, Bolivia), who was a team member during June and July; and Jose Tello (head of the CITES/Bolivia cat survey), who assisted the caiman survey teams in Beni and Pando. Juan Villalba-Macias (TRAFFIC/SudAmerica, Montevideo, Uruguay) lent valuable assistance in inventorying the tanned and finished hides in the ASICUSA warehouses, and in handling contact with government officials in La Paz. Candido Pastor (CDF, Cochabamba) and Heriberto Cardozo (Vida Silvestre, CDF, Santa Cruz) also participated in the hide inventory.

This survey would not have been possible without the encouragement and constant support of Dr. Obdulio Menghi (CITES Scientific Coordinator). Thanks are also due Roger Bazan Roca (former Director of Unidad Tecnica Desconcentrada CDF Santa Cruz), and Heriberto Cardozo (former Jefe of the Department of Vida Silvestre, Parques Nacionales, Caza y Pesca, CDF Santa Cruz), who assigned technical staff to the survey effort, loaned field vehicles to the project, made laboratory space available for storage of specimens and equipment, and assisted in many other less tangible ways.

Special thanks are extended to Víctor Paz Estenssoro, President of the Republic of Bolivia, and Juan Carlos Duran, past Ministerial Secretary and present Minister of the Interior, who repeatedly demonstrated their commitment to CITES, to wildlife conservation, and to the survey. Hector Mendoza Ruiz and Humbertos Hoyos C., past and present National Directors of CDF, La Paz; and Edil Sandoval Moron, past Minister of Asuntos Campesinos y Agropecuarios (Ministry of Rural and Agricultural Affairs), cooperated with the CITES Secretariat in developing and continuing the survey program.

The Asociación de Industriales de Cueros de Saurios (also known as the Asociación de Industrias de Curtiembre de Saurios, ASICUSA) contributed financial and continuing logistical support to the survey effort; special thanks are due to ASICUSA President Vladimir Khek (owner of Curtiembre Tomy, Cochabamba), and to members, Daniel Milicovsky (Curtiembre Alligator, Cochabamba), Dino D'Addario (Curtiembre Camba, Santa Cruz de la Sierra), Atilio Quaino and Juan Manuel Paz (Curtiembre Moxos, Trinidad), and Richard Rau Gomez and Oscar Alcocer (Curtiembre San Matias, San Matias and Santa Cruz de la Sierra), Carlos Claros Equez (Curtiembre Santa Cruz, Santa Cruz de la Sierra), and Ernesto David Pereyra (ASICUSA lawyer, Cochabamba).

Additional funding for the project was contributed by the U.S. Fish and Wildlife Service (U.S.A.); World Wildlife Fund (U.S.A.); the Government of Japan (Japan); the European Economic Community (EEC); Italtretille (Italy); All Japan Association of Reptile Skins and Leather Industries (Japan); Trading S.R.L. (Paraguay); U. Müller GMBH (Federal Republic of Germany); France-Croco (France); Tanneries et Cuirs d'Indochine (France); Fonseca Fur & Hide (U.S.A.); Syndicat National des Tanneurs de Reptile Français (France); John G. Mahler Co. (U.S.A.); and Bodipelli (Italy).

Mario Baudoin W. of the Instituto de Ecologia, Universidad Mayor de San Andres, La Paz, contributed time, language skills, and encouragement to the caiman survey and to efforts to build a cadre of professional wildlife biologists in Bolivia. Reginald Hardy of PRODENA and the Bolivian Wildlife Society assisted communications and helped maintain contact with government officials. Thanks are also due the many people whose hospitality and local assistance contributed to the success of the survey: Abel Gamara (in Riberalta), Mauricio Hauser (La Paz, San Borja, and Trinidad), Lambertos van den Eijnde (Cochabamba), Federico Bascope-Vargas and Victor Hugo Paz (Santa Cruz de la Sierra), Mario Challapa Zapata (Trinidad), Hilton Barja (Managing Engineer of Occidental Petroleum's Camp Tito), Ignacio and

David Solis (Florida), and Dr. Luis Felipe Hartmann L. (President of the Academia Nacional de Ciencias, La Paz).

The interest and support of the staffs of the Hotel Colonial, Santa Cruz de la Sierra, and the Hotel Ganadero, Trinidad, made our stays in those cities pleasant and much more productive.

Mrs. Rosario Henriques and Mrs. Nora Ferrel-Urquidi, of the International Passenger Section of Lloyd Aereo Boliviano in Santa Cruz de la Sierra, were enormously helpful in locating lost baggage and overcoming ticketing problems.

Finally, the survey might have been possible, but certainly would have been much more arduous an undertaking, had it not been for the many citizens of Bolivia, who, after a brief explanation of what the survey team was trying to accomplish, accepted the team members into their midst (and occasionally into their homes), proffered logistical support, and supplied much valuable information.

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DRAFT

RESOLUTION OF THE CONFERENCE OF THE PARTIES

Implementation of the Convention in Bolivia

RECOGNIZING the concern for international compliance control expressed in Resolution Conf. 3.0, adopted at the third meeting of the Conference of the Parties (New Delhi 1981);

RESPONDING to the call for Bolivia to implement and effectively comply with the requirements of the Convention as contained in Resolution Conf. 5.2, adopted at the fifth meeting of the Conference of the Parties (Buenos Aires 1985), including a reduction of wildlife exports to 50% until on the population and on the environmental impact studies have been completed, and management programs established;

NOTING that, as indicated in Doc. 6.20 Implementation of the Convention in Certain Countries, prepared by the Secretariat; Bolivia has not been able to effectively implement the Convention, despite support from the highest levels of the its Government;

CONSIDERING that since the fifth meeting of the Conference of the Parties (Buenos Aires 1985), the Government of Bolivia repeatedly has made administrative changes in its wildlife agency in a continuing effort to build a CITES program and enforce its provisions;

ACKNOWLEDGING that, in partial fulfillment of Conf. 5.2, population surveys of caimans and felids have been initiated under a cooperative agreement between Bolivia's Centro de Desarrollo Forestal and the CITES Secretariat;

BELIEVING that agreeing to utilize an expatriate specialist, selected by the CITES Secretariat, to assist in the development of a CITES program is a demonstration of the desire of the Government of Bolivia to comply fully with the provisions of the Convention;

RECOGNIZING that Bolivian law only permits the hunting of Lagarto (*Caiman yacare*) more than 1.5 m in total length, which yields a belly or hornback hide of the same length or two flank hides 80 cm or more in length;

FURTHER RECOGNIZING that Bolivian law prohibits the export of raw or crusted (= semi-tanned) caiman hides, and only permits the export of finished (= fully tanned, dyed, and glazed) caiman hides and hide products by one of the six tanners belonging to the Asociación de Industriales de Cueros de Saurios (ASICUSA);

APPLAUDING the decision by ASICUSA members to assist the Parties to the Convention to identify legal exports of caiman hides from Bolivia by indelibly stamping the reverse side of their hides with the name of the tannery that processed the hides; and by having their CITES permitted export shipments certified and sealed by the Société Générale de Surveillance, a Swiss company specializing in customs control;

AWARE that Bolivia cannot implement CITES unless the Parties to the Convention actively support its efforts by denying entry to shipments of hides exported in contravention of Bolivian law and CITES regulation;

THE CONFERENCE OF THE PARTIES TO THE CONVENTION

RECOMMENDS that countries receiving wildlife and wildlife products from Bolivia assure that each shipment is accompanied by CITES export permits as required under the provisions of the Convention, and in the case of caiman hides, as an additional guarantee that the shipment was legally exported, the importing nation should:

- 1) allow only the entry of finished (= fully tanned, dyed, and glazed) caiman hides and hide products,
- 2) only if the shipment has been certified and sealed by the Société Générale de Surveillance, and
- 3) only if it was shipped by one of the members of the Asociación de Industriales de Cueros de Saurios (ASICUSA).

EXHORTS neighboring countries not to allow dealers in illegal wildlife to operate openly within their jurisdictions; and

URGES the Parties to the Convention not to encourage illegal trade by allowing imports from dealers in illegal wildlife from nations neighboring Bolivia.

Table 1.

| Wetland | Bank or Shoreline | Estimated density /km of shore | Size Range (in m) |
|--|--|-----------------------------------|----------------------|
| A. Beni river, above Cachuela Esperanza | Mud banks with some overhanging vegetation | 0.0 | .--- |
| B. Beni river, downstream from Riberalta | Bare mud and logs | 0.1 | .--- |
| C. Yata river, a tributary of the Beni | Bare mud & well vegetated banks & floating mats | 0.25 | 0.5-1.1 |
| D. Itenez river, near Versalles | Well vegetated | 0.75 | 0.3-0.5 |
| E. San Pablo river, upstream portion of the San Miguel/Itonamas river | Bare mud & well vegetated banks | 0.0 | .--- |
| F. Ipurupuru river, a tributary of the Machupo river flowing into the Itenez | Overhanging vegetation | 1.5 | 1.0-1.5 |
| G. Ibare river, in vicinity of Trinidad | Bare mud | <0.5 | 0.3-0.5 |
| H. Yapacani river, a tributary of the Mamore | Bare mud & sand | 1.5 | 0.3-1.0 |
| I. Embayment off the Itenez river, upstream from Versalles | Well vegetated & floating plants | 2.65 | 0.6-1.0 |
| J. Embayment off the Paragua river, a tributary of the Itenez | Well vegetated & floating plants | 1.25 | 0.6-2.0 |
| K. Laguna Concepción, west of San Jose de Chiquitos | Well vegetated & floating plants | 4.0 | 0.6-1.0 |
| L. Lago San Jose, near Riberalta | Well vegetated | 70.0 | 0.3-2.0 |
| M. Unnamed lagoon, off the Mamore, upstream from Santa Ana | Well vegetated & floating plants | 1.0 | 1.2 |
| N. Arroyo Biajo, a curichi off the Mamore | Well vegetated | 1.25 | 1.0-1.2 |

Table 1 Continued.

| Wetland | Bank or Shoreline | Estimated density /km of shore | Size Range (in m) |
|---|-------------------------------------|-----------------------------------|----------------------|
| O. Yagaru, north of Ascension de Guayaros | Well vegetated & floating plants | 0.4 | 1.0-1.5 |
| P. San Miguel reservoir, near San Ignacio de Velasco | Well vegetated & floating plants | 0.2 | 2.0 |
| Q. Roadside borrow pits near Reyes | Well vegetated | 1.5 | 1.0 |
| R. Roadside ditches with permanent water near Trinidad | Well vegetated | 3.3 | 0.8-1.5 |

A. through H. are riverine localities with flowing water; I. through K. are shallow, quiet water embayments off the main channel of the river; L. through O. are oxbow lakes and lagoons formerly broadly connected to the river, but now slightly separated; and P. through R. are man-made wetlands. Within each of these categories, the localities are listed roughly from the north to the south.

GENETIC PATTERNS AND THE CONSERVATION OF CROCODILIANS: A REVIEW OF STRATEGIES AND OPTIONS

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ABSTRACT - Recent developments in the field of ecological genetics are described and the literature is reviewed with respect to studies of crocodilians. The development of starch gel electrophoretic techniques has provided a relatively simple means of surveying levels of genetic variability in both captive and wild populations and also for determining the degree of genetic relatedness between populations. Applications of these techniques to programs of captive propagation and the management of wild crocodilians are discussed. Of particular interest are techniques for determining paternity in mixed captive breeding groups and identification of racial or geographic origins of individual animals. Positive correlations between levels of genetic variability and the general vigor and reproductive output of individual animals of several species suggest that electrophoretic genetic surveys could help to suggest ways in which these traits could be optimized in both captive and wild populations of crocodilians.

INTRODUCTION

Recent advances in the field of population genetics have provided a number of useful techniques for the management and conservation of both captive and wild populations of various species (Manlove et al. 1975, 1976; Selander 1983; Smith et al. 1976; Johns et al. 1977; Smith et al. 1978; Chessier et al. 1980; Chambers and Bayless 1983; Harris et al. 1984; Vrijenhoek et al. 1985; Meffe 1986). The use of horizontal starch gel electrophoresis, in particular, has provided a means for rapid and inexpensive assessment of the degree of genetic relatedness between populations. It has also provided a means to assess both temporal and spatial patterns of genetic variability (Chessier et al. 1982). This information can then, in turn, be used to determine the extent to which programs of captive propagation may have altered the naturally-occurring patterns and levels of genetic variability of wild populations.

The purpose of this report is to briefly summarize the genetic information currently available for crocodilians and then to examine the implications of these studies for both captive propagation and management of wild populations. First, however, it will be useful to review the basic principles behind the multi-locus approach to biochemical analyses of population genetic parameters.

BACKGROUND GENETIC INFORMATION

Crocodilians, like most sexually-reproducing organisms, receive two copies of each chromosome and therefore two alleles at each gene locus, one from each parent. If the alleles received from each parent are

identical, the individual is said to be homozygous for that particular gene locus. If different alleles are received from each parent, the individual is said to be heterozygous, and the locus is described as being polymorphic. It should be remembered, however, that in the case of allelic dominance, it is possible for both a homozygous dominant and a heterozygous individual to be phenotypically identical from the point of view of external physical appearance. Under such conditions, it would not be possible to directly determine the frequency of the various alleles in the population on the basis of external phenotypes alone, since the expressions of recessive alleles could be "masked" by the dominant phenotypes of heterozygous individuals.

In such situations, techniques such as starch gel electrophoresis are of key importance; by demonstrating the presence of the gene products of otherwise phenotypically recessive alleles as codominants, in heterozygous individuals, such procedures provide a means of directly quantifying the frequency of alternative alleles within population samples. The determination of such gene frequencies thus provides the means by which hypotheses concerning genetic relatedness between populations may be tested statistically (Chesser 1980).

LITERATURE REVIEW

Only three current publications provide information concerning levels and patterns of genetic variability in crocodilians and all of these papers deal with the American alligator (*Alligator mississippiensis*). Gartside et al. (1977) report from southwestern Louisiana, while Menzies et al. (1979) provide similar information for alligators from the Everglades National Park in Florida. Adams et al. (1980) provide the only direct comparisons of alligator populations from three different parts of the species range, providing genetic data from alligators in South Carolina, Loxahatchee National Wildlife Refuge in Florida and from the same general region in southwestern Louisiana as that studied by Gartside et al. (1977). A comparison of gene frequencies calculated for the Louisiana alligators indicates close agreement between the results from these two studies which were conducted independently at different laboratories. Adams et al. (1980), for example, report a frequency of 0.77 for the common allele of lactate dehydrogenase-2 while Gartside et al. (1977) report a comparable value of 0.81 for this same allele from Louisiana alligators. This suggests that the use of electrophoresis can produce results which are comparable and independently replicable between laboratories.

In every case where gene frequencies have been compared between alligator populations, the populations in question have been found not to share a common gene pool. Thus, Menzies et al. (1979), in comparing their results with those published earlier by Gartside et al. (1977), found that the Everglades alligator population was genetically different from those of southwestern Louisiana, as described by the latter authors. Similarly, Adams et al. (1980) report that every gene locus examined in their study that had a frequency of 0.15 or greater for the alternate rare allele, showed a statistically significant spatial heterogeneity. For example, Chi-square testing of count data for the allele frequencies of lactate dehydrogenase-2 showed that differences in gene frequencies between the three alligator populations could not be accounted for by chance variation alone, thereby inferring that the three populations in question did not share a common gene pool (Fig. 1).

Even though all wild alligator populations that have been studied so far have been found to be genetically different, the overall degree of genetic divergence between populations is relatively small (Adams et al. 1980). Multi-locus electrophoretic data can be used to quantify the degree of genetic divergence between populations through the calculation of one or more indices of genetic separation. The calculation of Rogers' index of genetic distance (Rogers 1972) by Adams et al. (1980), for example, revealed that values quantifying the degree of genetic separation between alligator populations (range: 0.018 - 0.081; Fig. 2) were all relatively low in comparison to similar values for conspecific populations which may range as high as 0.15 (Selander and Johnson 1973; Avise 1974, 1976).

Lactate Dehydrogenase -2
 ($\chi^2 = 16.61$; $P \leq 0.001$)

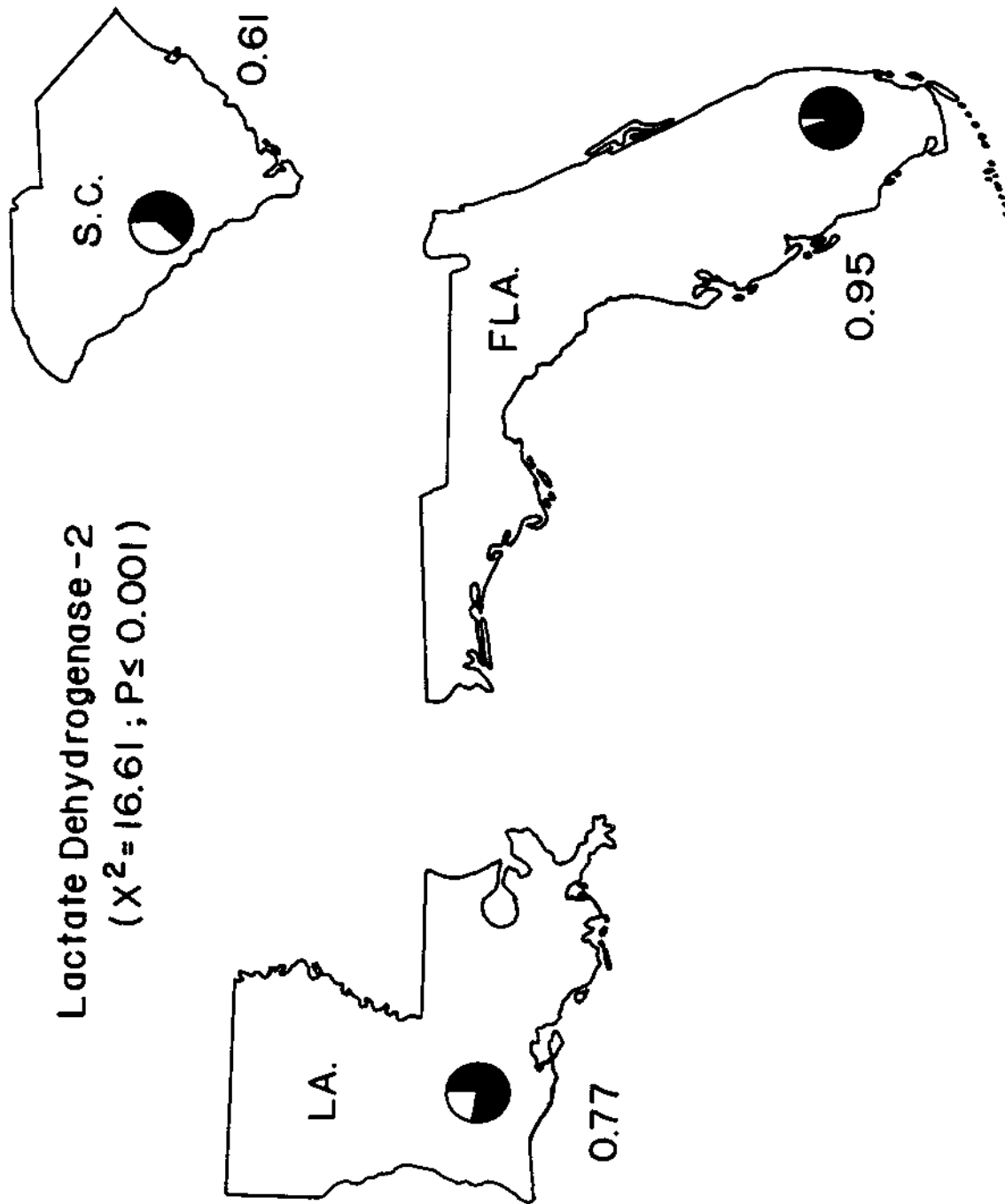


Figure 1. Frequencies of two alternate alleles of the gene encoding lactate dehydrogenase-2, as determined by electrophoretic analyses of tissue samples from American alligator populations in three southeastern states. Blackened portions of each pie diagram represent the frequency of the common allele in each population. Chi-square analyses indicate that the three populations in question do not share a common gene pool. (Drawn from data presented by Adams et al. 1980).

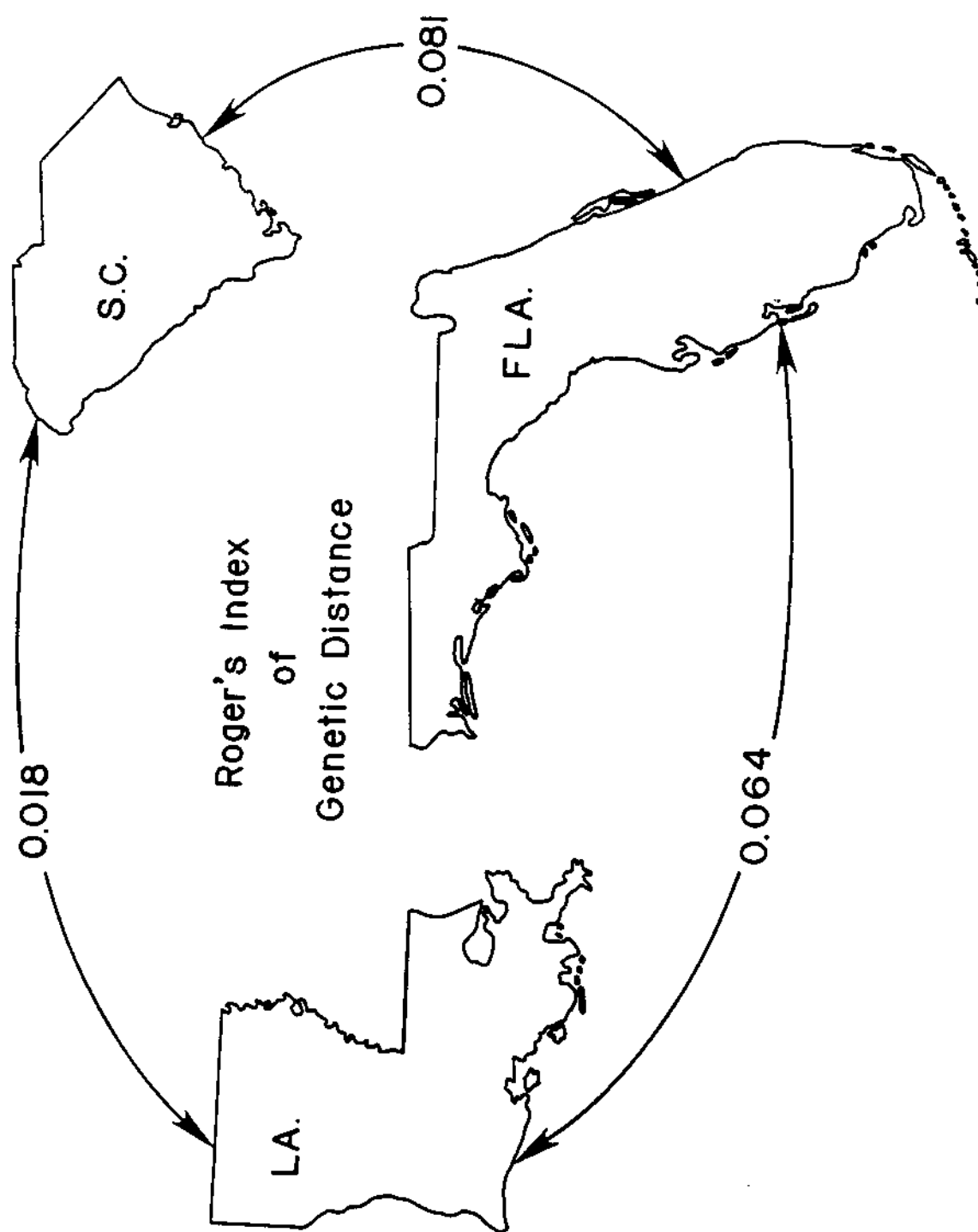


Figure 2. Roger's index of genetic distance between populations of American alligators from three southeastern states. Indices were calculated on the basis of electrophoretic analyses of tissue samples. (Drawn from data presented by Adams et al. 1980).

Table 1. Comparisons of literature values quantifying levels of genetic variability in populations of the American alligator in the southeastern United States.

| Population | Number of Loci | Proportion of Loci which are Variable (P) | Average Heterozygosity per Individual (H) (± 2 S.E.) | Reference |
|---|----------------|---|---|------------------------|
| Southwestern Louisiana | 49 | 0.06 | 0.021 (± 0.024) | Gartside et al. (1977) |
| | 27 | 0.074 | 0.012 (± 0.004) | Adams et al. (1980) |
| Florida: Everglades National Park | 44 | 0.045 | 0.0086 (± 0.016) | Menzies et al. (1979) |
| Florida: Loxahatchee National Wildlife Refuge | 21 | 0.19 | 0.02 (± 0.006) | Adams et al. (1980) |
| South-central South Carolina | 27 | 0.19 | 0.034 (± 0.006) | Adams et al. (1980) |

Several different indices may be calculated to quantify and compare the overall degree of genetic variability within and between species populations. These indices include P, the proportion of all loci examined which are variable (i.e., show more than one allele) and A, the average number of alleles per locus (Adams et al. 1980). Probably the most useful index of overall genetic variability, however, is H, the average heterozygosity per individual. H represents the population average of the number of heterozygous loci over the total possible loci assayed per individual. Heterozygosity, then, is distinct from P, which measures the potential variability at loci in the population sampled, whether or not these loci are heterozygous for any individual. Because statistical procedures are available for calculating confidence limits for estimates of heterozygosity (e.g., Nei and Roychoudhury 1974), this index is particularly useful for comparing levels of genetic variability between populations.

A comparison of all available values for H and P which have been calculated for alligator populations are presented in Table 1. As pointed out by Adams et al. (1980), values of H for alligator populations are quite low in comparison to those of other non-mammalian vertebrate species (Nevo 1978, Nevo et al. 1983). Lewontin (1974) and Selander and Johnson (1973) indicate that heterozygosity values typically range from 0.05 to 0.18. All alligator heterozygosity values are below the lower limit of this range (Table 1). However, Adams et al. (1980) point out that most of their P values for alligator populations (Table 1) are within the range typically reported for other vertebrates (0.1-0.2; Avise 1974). The former authors suggest that this observed pattern of relatively high P values in combination with low values for H, would be reasonable for a species such as the alligator with a large geographic range and limited gene flow between populations (resulting in a higher P), in combination with a large body size and relatively small breeding populations (which typify species with a relatively low H). These data need to be interpreted with some caution. H and P are not independent of one another. H is also sensitive to other variables not traditionally standardized among electrophoretic studies, such as the type of enzymes assayed, enzyme function and molecular size (Johnson 1974, 1976; Ward 1977). As an example of problems that may arise in interpretations of comparisons of genetic variability across studies, Simon and Archie (1985) demonstrated that subsampling

enzymes from a study of 38 loci in the milkfish, *Chanos chanos*, produced a range of heterozygosity values from 5.6% to 11.4%. These values include the differences in means between vertebrates and invertebrates found in Nevo's (1978) analysis of 227 species. Therefore, we recommend comparisons across studies be made for a standardized set of loci.

For the present, we must rely on H, P, and A as the necessary indices of genetic variability within and across populations, and keep in mind that conflicting hypotheses may be the result of artifacts in our ability to measure variability accurately at this time. The pros and cons of supplementary, complementary or contradictory hypotheses to explain the observed patterns of genetic variability in alligator populations have also been discussed by others (Gartside et al. 1977; Menzies et al. 1979). These hypotheses include genetic "bottlenecking" and genetic drift during periods of low population numbers, environmental grain, and directional selection, all of which may help to explain the observed patterns of genetic variability. More information concerning long-term patterns of gene flow between alligator populations is needed, however, before the roles of such hypotheses can be properly evaluated (Adams et al. 1980). To complicate the issue further, low levels of heterozygosity may be characteristic of some taxa, but may be the result of population bottlenecking for others. The cattail genus *Typha* is homozygous for all 10 loci examined (Mashburn et al. 1978), largely because of its clonal method of reproduction. On the other hand, the northern elephant seal (Bonnell and Selander 1974) experienced a drastic population reduction at the turn of the century. They have now recovered in population numbers, but still show no genetic variation at the 24 loci examined. The cheetah, *Acinonyx jubatus*, (O'Brien et al. 1983, 1985; Wayne et al. 1986) also shows little genetic variation, and this has been attributed to an unobserved bottleneck since the Pleistocene. The low levels of heterozygosity in both of these mammalian examples may be the result of the real or inferred bottlenecks, with prolonged recovery predicted by population genetics theory, (Nei et al. 1975), or, alternately, they may be a result of the demographic strategies of these particular species. Sibley and Ahlquist (in press) suggest, with their data on birds, that some groups show slower rates of molecular evolution. These slower rates seem to be correlated with longevity, later age to first reproduction, and fewer young produced per reproductive effort. These demographic factors may feed back into the overall genetic variability of the species as a whole, resulting in fewer mutations being incorporated per generation, and consequently, less genetic variability (Gilpin and Soule 1986). If this is the case, then species like the alligator may have always had low levels of heterozygosity and have adapted to the low variability through demographic factors, such as dispersal.

What this means is that there are many factors influencing genetic variability, and numerous ways that genetic variability can influence the success of a species (Nevo 1978). We have little understanding of how the organization of the genome influences the long-term survival of a species, which in turn, influences the short-term genetic variability (Meffe 1986). We need more basic research in natural population structure and effects of genetic variability on the viability of populations. A more thorough understanding of genome organization - such as the role of introns, regulators, transposable elements and the like - will make it easier to comprehend the differing strategies species employ in responding to their environment. We concur with policies based on efforts to remain conservationally conservative; that is, efforts should be made to retain as much genetic variability as possible, regardless of how basic our techniques are, until we are better able to understand the influence of genetic variability on the health and survival of the species being managed. Additionally, we must always keep in mind that outbreeding depression may be as problematical as inbreeding depression (Templeton 1986; see below).

An examination of the levels of heterozygosity calculated for all available studies of alligators (Table 1) suggests that while there may be considerable variation in the degree of heterozygosity shown by different alligator populations, there is a broad general overlap of the 95% confidence intervals (+ 1.96 S.E.) about these estimates, and indeed, the magnitude of these confidence intervals may themselves show considerable variation. Part of the differences in the sizes of confidence intervals about estimates of heterozygosity for alligator populations may be due to differences in the techniques used in their computation. Adams et al. (1980) used standard parametric statistical procedures to calculate their confidence limits, (but see Archie 1985) while Gartside et al. (1977) used the method of Nei and Roychoudhury (1974). Nevertheless, the data for heterozygosity presented by Adams et al. (1980; Table 1)

suggest that the alligators from their South Carolina sample may have had a significantly higher level of average genetic variability than those from Louisiana.

APPLICATIONS OF GENETIC STUDIES

As discussed earlier, genetic studies may have direct application to two main aspects of concerns for crocodilian conservation: (1) management of wild populations, and (2) development of programs of captive propagation. The present and possible future contributions of studies using starch gel electrophoretic techniques will be discussed for each of these areas separately.

Management of Wild Populations: A model for the application of genetic studies to the management of free-living wildlife populations is provided by Manlove et al. (1975) and Smith et al. (1978), for management of the white-tailed deer (*Odocoileus virginianus*). As pointed out by these authors, electrophoretic studies of blood and/or tissue samples can, through the calculation and comparison of gene frequencies across space and time, help to define functional management units in terms of population cohorts sharing common gene pools. The definition and delineation of such management units is, of course, a critical prerequisite for devising management plans for a species across its range of geographic occurrence. As an example, the failure of nesting populations of loggerhead sea turtles (*Caretta caretta*) to share a common gene pool between coastal barrier islands of South Carolina and Georgia (Smith et al. 1978), indicates that intensive management efforts designed to help this species on one island would probably have little or no effect on nesting populations on some other islands in the same southeast region. Similar arguments may be made for management programs designed for crocodilian populations which are also comprised of spatially discrete genetic units, as illustrated by Figure 1.

Another potential value of genetic studies for the management of wild populations lies in the possibility of identifying so-called "marker" genes which may help to identify the racial or geographic origin of individuals found in captive collections or confiscated through law enforcement activities. In the case of the three alligator populations studied by Adams et al. (1980), for example, electrophoretic studies of the blood from a confiscated animal found in a shipment illegally destined for export might reveal the presence of the uncommon allele of peptidase-1, which is found in 16% of the Florida alligators, but which is absent from the populations in South Carolina or Louisiana (Fig. 3). This would indicate a Florida origin for the specimen in question, if these were the only populations under consideration. Obviously, the usefulness of this technique will be increased in proportion to the number of different population units that can be surveyed from throughout the species range. It should also be remembered, however, that in the example cited above, 84% of the Florida animals could not be separated from those from the other two states on the basis of the peptidase-1 system alone. Thus, the greater the number of electrophoretically variable systems that can be demonstrated for a given species, the more likely it is that this procedure will be able to positively identify the population of origin for a given individual.

Finally, as demonstrated by Ryman et al. (1981), the precise forms of management and harvest schemes which may be proposed for a given species can significantly alter both its patterns and levels of genetic variability and thereby alter the roles of any factors related to this variability as discussed in this report. Such possibilities must be borne in mind when devising management schemes and quotas for the sustained-yield harvest of species such as the American alligator (Nichols et al. 1976). Of particular concern in this regard would be the possibility that improper harvest schemes might, through the inadvertent alteration of population sex ratios and/or age structure, reduce effective population size and thereby increase the probability of a reduction of overall genetic variability (Ryman et al. 1981; Gilpin and Soule 1986).

Programs for Captive Propagation: The general application of genetic studies to the captive propagation of endangered species have been outlined by Chesser et al. (1980). While specific examples chosen by these authors are taken from the zoo literature on captive-breeding populations of ungulates and field studies of

Peptidase -1
($\chi^2 = 15.39$; $P \leq 0.001$)

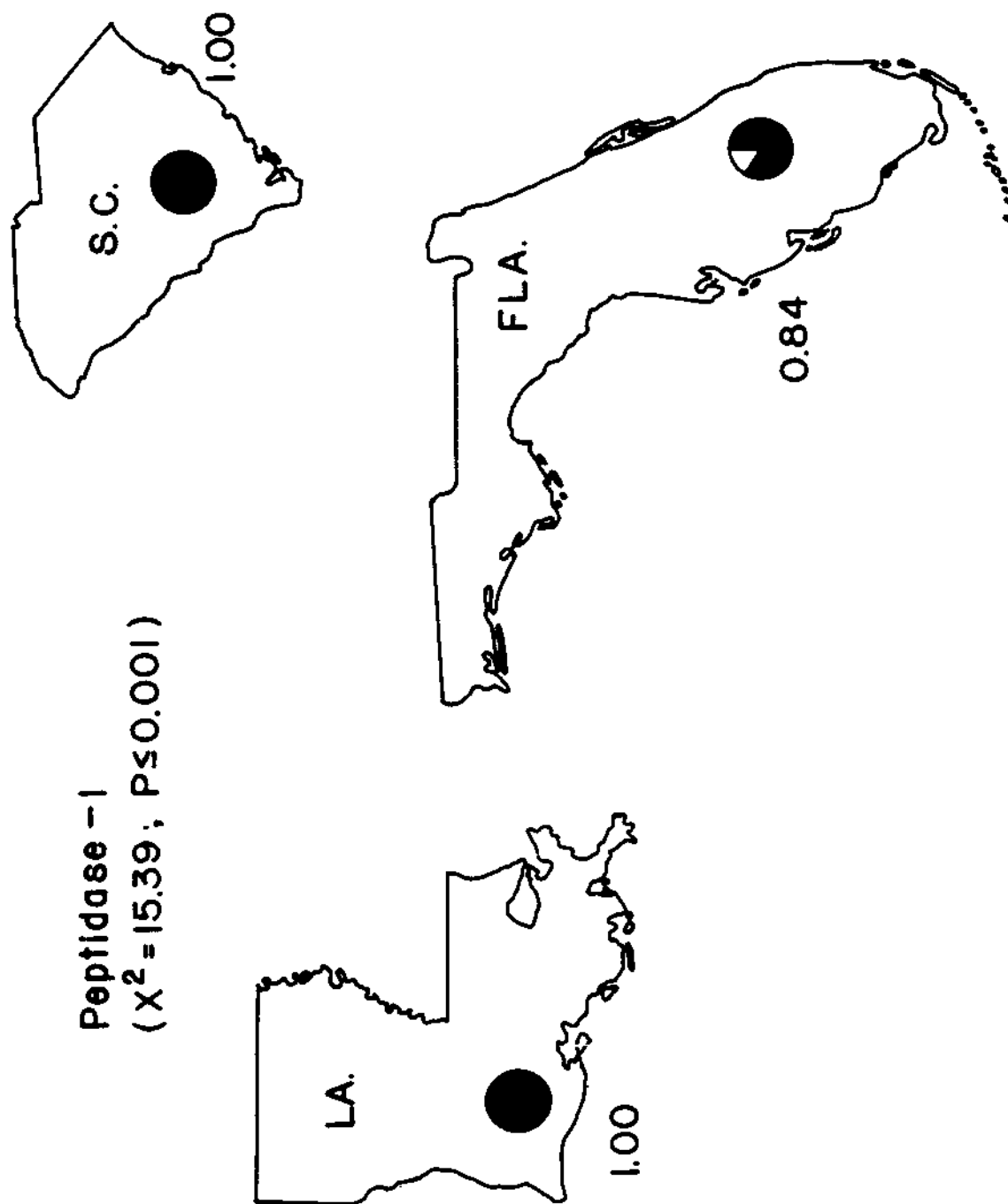


Figure 3. Frequencies of two alternate alleles of the gene encoding peptidase-1, as determined by electrophoretic analyses of tissue samples from American alligator populations in three southeastern states. Blackened portions of each pie diagram represent the frequency of the common allele in each population and indicate the potential for the use of the rarer allele from the Florida population as a "marker gene" to help to identify specimens of unknown geographic origin. (Drawn from data presented by Adams et al. 1980).

the genetics of white-tailed deer, many of the general principles presented are also applicable to the captive propagation of crocodilians. A generalized breeding scheme has been proposed by these authors, which would preserve maximum amounts of genetic variability in captive breeding populations. This scheme closely mimics the general procedures by which most species of crocodilians are currently being bred in either zoos or in more specialized farming operations - namely, the maintenance of relatively small closed breeding populations in which the loss of genetic variability and fixation of rare alleles would occur at a relatively rapid rate. In order to avoid deleterious effects of the inbreeding depression that may occur in such situations (Ralls et al. 1979), breeding stock should then be exchanged between zoos or farms to increase outbreeding. Such outbreeding should occur at pulsed intervals, which are determined by the times at which the greatest reversal of the deleterious effects of inbreeding depression can be achieved.

In selecting breeding stock for exchange, profitable use can be made of electrophoretic genetic profiles which would indicate which matings would produce the greatest increase in overall heterozygosity. As will be pointed out later, there is evidence that significant increases in general vigor, viability and reproductive output can be expected to be associated with pairings that maximize levels of heterozygosity in the offspring (Mitton and Grant 1984). In order to realize these goals, Chesser et al. (1980) emphasize that the actual choice of animals as breeders should be made at random, within the guidelines suggested by electrophoretic genetic profiles. In larger breeding groups, such as are often maintained in commercial crocodilian farming operations, allowing animals to select their own mates allows a closer approximation of some of the selective forces which may be operative in wild populations of the same species. The preservation and exchange of frozen semen between institutions (Anon. 1980) can also produce a pulsed outbreeding which can counteract the effects of inbreeding depression.

Starch gel electrophoretic studies can also be of importance in helping to evaluate the degree to which captive breeding programs have been successful in approximating the levels and patterns of genetic variability actually found in wild populations. Thus, the fact that reduced levels of heterozygosity may be found in certain captive breeding groups need not necessarily be a cause for concern - particularly if the genetic surveys of successful wild populations of the same or closely related species should also reveal similarly reduced levels of heterozygosity. If, for example, a genetic survey of the few available captive Chinese alligators (*Alligator sinensis*) should reveal low heterozygosity values of 0.005 - 0.010, this fact in itself would not necessarily be a cause for concern since it has now been shown that vigorous and viable populations of wild American alligators may have heterozygosity levels that are not any higher (Gartside et al. 1977; Menzies et al. 1979; Adams et al. 1980; Table 1).

Still another potential application of genetic analyses to captive breeding programs lies in the ability of such studies, under appropriate conditions, to identify those individuals which are actually siring offspring in large mixed breeding groups. Such information could be of great practical value since it would allow the identification of non-breeding males which could then be removed from such breeding groups and either disposed of or transferred to other breeding groups where the social structure or other factors might permit them to start mating and producing offspring. As in the case of identifying unknown individuals as to racial or geographic origin on the basis of electrophoretic profiles, the probability of successfully using this same technique to identify paternity will be increased in proportion to the number of electrophoretically detectable variable gene loci that can be identified. A total of ten variable gene loci have already been demonstrated for the American alligator using starch gel electrophoresis (Gartside et al. 1977; Adams et al. 1980) and while the demonstration of more variable loci would be helpful, useful paternity information could now be collected in appropriate situations, with the use of only those ten variable gene loci which have already been demonstrated for this species.

Finally, one of the most exciting and potentially useful aspects of electrophoretic genetic surveys of captive breeding populations lies in the fact that certain traits related to the maximization of reproductive output and the maintenance of health and vigor have been shown to be positively correlated with increased levels of genetic variability in certain environments (Mitton and Grant 1984; Allendorf and Leary 1986). Significant relationships have been found, for example, between genetic variability and higher reproductive rates (Smith et al. 1975; Johns et al. 1977), higher growth rates (Singh and Zouros 1978) and increased

levels of aggression and dominance (Garten 1976). These studies suggest a pattern which, if it holds for crocodilians as it has been shown to hold for other species such as shellfish and deer, could provide a means for making effective decisions concerning the selection of breeding animals for either captive matings, release and restocking into wild populations, or transfer between wild population subunits. The implications of these genetic studies for the captive management and propagation of endangered species in a general sense have been discussed by Chesser et al. (1980). Alternately, if populations are so small that there is no hope of avoiding inbreeding depression, then the only recourse would be to force the population through a controlled bottleneck in order to purge it of deleterious alleles, as was done for the Speke's Gazelle (Templeton and Read 1983). Moreover, if crocodilians are predisposed to strong population structuring at local levels but population mixing at regional levels (Fig. 2), then programs attempting to enhance outbreeding may result in outbreeding depression, where coadapted gene complexes are broken up, to the detriment of the locally adapted population (Alstad and Edmunds 1983; Templeton 1986). Starch gel electrophoresis can help us decide which strategy to follow in our conservation efforts.

As illustrated by the foregoing examples, the majority of genetic studies related to the management of wild populations and captive propagation have not yet dealt directly with crocodilians. However, those genetic surveys that have been undertaken with the American alligator indicate that this species and thus possibly other species of crocodilians as well, can also be profitably studied with the use of starch gel electrophoresis, using blood and/or tissue samples which can be collected with little or no risk of harm to the animal involved. The collection of such genetic information from larger numbers of individuals and from additional species of crocodilians could not only contribute significantly to the wise management, captive propagation and conservation of such crocodilian species themselves, but could also provide valuable data which could help to increase our general understanding of the population genetics of many kinds of wildlife species throughout the world.

ACKNOWLEDGEMENTS

The authors are grateful to Toni L. DeSanto, Gary K. Meffe, James M. Novak, Michael H. Smith, Nils Ryman and Ron Chesser for helpful discussions and suggestions during the preparation of this manuscript and for critical readings of an early draft. This manuscript was prepared under the support of contract DE-AC09-76SR00819 between the United States Department of Energy and the University of Georgia.

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APPLICATIONS OF LIMNOLOGY AND HYDROLOGY TO CROCODILIAN CONSERVATION AND MANAGEMENT

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SUMMARY

Limnological data were gathered from 7 *Paleosuchus trigonatus* localities, 15 *Caiman crocodilus* localities, and 7 *Caiman crocodilus* (Llanos subspecies) localities. The mean temperatures (C), conductivities (MHOS) and total cations (ueq/l) were 22.4/6.6/49.3, 29.1/48.5/215.8, and 32.4/125.6/1,052.2 respectively. Hydrological data were processed for 27 *Crocodylus intermedius* localities and 16 *P. trigonatus* localities. Mean annual rainfall (mm) and runoff (mm) were 1,797/734 and 2,422/1,441 respectively. It is suggested that these correlations indicate ecological relationships between habitats and crocodilians. Limnological and hydrological data are easily obtainable, and could be applied to survey planning, ecological studies, site selection for reintroductions, and environmental impact assessment.

RESUMEN

Se recolectó información limnológica en 7 localidades de *Paleosuchus trigonatus*, 15 de *Caiman crocodilus crocodilus*, y 7 de *Caiman crocodilus* de Llanos. Los promedios de temperaturas (C), conductividades (MHOS) y cationes totales (ueq/l) fueron 22.4/6.6/49.3, 29.1/48.5/215.8, y 32.4/125.6/1,052.2 respectivamente. Información hidrológica fue procesada para 27 localidades de *Crocodylus intermedius* y 16 de *Paleosuchus trigonatus*. Los promedios de lluvias anuales (mm) y escurrimientos anuales (mm) fueron 1,797/734 and 2,422/1,441 respectivamente. Se sugiere que estas correlaciones indican relaciones ecológicas entre hábitats y crocodilidos. La información limnológica e hidrológica es fácilmente obtenible, y podría ser aplicada en inventarios, estudios ecológicos, selección de sitios para reintroducciones, y evaluación de impacto ambiental.

INTRODUCTION

In Venezuela government and non-government organizations are working on a conservation program of the Orinoco crocodile (*Crocodylus intermedius*), and on a smaller scale for the American crocodile (C.

acutus). An experimental harvest has been carried out with the spectacled caiman (*Caiman crocodilus*). The two other species of crocodilians, Schneider's smooth-fronted caiman (*Paleosuchus trigonatus*) and Cuvier's smooth-fronted caiman (*P. palpebrosus*) are poorly known.

Effective management and conservation plans for crocodilians require knowledge about the geographical distributions and the ecology of the species under consideration. In Venezuela (with a surface area of almost 1,000,000 km²) there are no records of any crocodilians being present in 72% of the country, although many such areas probably contain crocodilian populations. This implies that extensive surveying of crocodilians is a research priority in the short term. However, traditional surveying techniques need time, money and people. In this paper we present some preliminary data on limnological and hydrological characteristics of the habitats of three species of crocodilians. The results suggest that some easily obtainable data may help to define more precisely the habitats of individual crocodilian species, and thus facilitate survey planning and other related studies.

MATERIALS AND METHODS

Nomenclature - Medem (1983) recognizes the existence of various demes in the subspecies *C. crocodilus crocodilus* and discusses the unpublished revision that was begun by the late Karl P. Schmidt of the Chicago Natural History Museum, who had intended to describe the form from the Llanos of Venezuela and Colombia as a new subspecies (*C. c. humboldti*). Gorzula (1987) notes that there are differences in behavior, population structure, population dynamics and average size of adults between *C. crocodilus* from the Llanos and the Venezuelan Guayana. In order to distinguish between what are most probably two distinct subspecies, in this paper *C. crocodilus* from the Venezuelan Llanos is referred to as *C. crocodilus* (Llanos) and *C. crocodilus* from Venezuelan Guayana as *C. c. crocodilus*.

Study Sites and Limnology Data - Seven water samples of *P. trigonatus* habitat were collected at different sites in the Gran Sabana and Rio Carrao (Fig. 1). Fifteen water samples of *C. c. crocodilus* habitat were taken from the El Manteco area (Gorzula 1978) and in areas to the southwest of Ciudad Guayana (Fig. 1). Water samples were taken from *C. crocodilus* (Llanos) habitat at seven sites in the Venezuelan Llanos in the ranches (Hatos): Masaguaral and Terecay (Fig. 1). Detailed locality data (name, geographical coordinates, altitude in meters above sea level, date and time the samples were taken) are given in the appendix.

Superficial water samples were taken directly into 0.25 l plastic bottles. The following measurements and determinations were carried out in the field: air and water temperature, pH and conductivity. For laboratory analyses the samples were filtered through membrane filters or precombusted glass filters (Paolini et al. 1983).

Hydrological Data - The exact locations of 27 *C. intermedius* localities and 16 *P. trigonatus* localities were obtained from Ayarzagüena (pers. comm.), Fitzgerald (pers. comm.), Franz et al. (1985), Godshalk (1978), Gorzula and Paolini (1986), Ludlow (pers. comm.), Ramo and Busto (1986), Sequías (pers. comm.), Taphorn (pers. comm.), and direct observations by two of us (JT and SG).

Geographical coordinates and elevations were calculated from 1:100,000 and 1:25,000 scale maps of Venezuela (MARNR, 1979). Catchment areas above the locality were calculated from maps of scales 1:1,500,000 to 1:25,000 depending on the size of the river basin.

Rainfall and runoff data was taken from COPLANARH (1972) and the EDELCA data base. Flow rates were estimated by calculation from the existing data for the river basin or interpolated from data for adjacent basins.

RESULTS AND DISCUSSION

Limnology - Table 1 shows the mean values and standard deviations for the eight parameters that were measured for habitats of *P. trigonatus*, *C. c. crocodilus* and *C. crocodilus* (Llanos). The limnological results for individual localities are given in the appendix.

Apart from pH, the data for all other parameters separate out into three distinct groups, showing only small overlaps in the standard deviations of 3 of the individual cations (Ca^{++} , Na^{+} and K^{+}).

Apart from a single low value of pH 4.2 for *P. trigonatus* and a single high value of pH 9.3 for *C. crocodilus* (Llanos) the values for all three crocodilians are in the same general range from pH 5 to pH 7. However, the acidity of a body of water may be due to one or more independent factors. An increase in cations usually results in a tendency towards a higher pH, but an increase in CO_2 will lower the pH. Thus, in enclosed bodies of water it may be important to take oxygen concentrations into account. In rivers and streams that drain off from forested areas or peat bogs (such as in the Gran Sabana) high concentrations of organic acids will also lower the pH (Folster, pers. comm.). Thus, for this parameter further sampling may change the initial picture.

The differences in mean temperatures of the three crocodilian habitats may be partly explained by the effect of an altitudinal gradient in that the localities for *P. trigonatus* are highland sites from 450 to 940 m, whereas all the other localities are below 300 m. It is interesting to note that Magnusson et al. (1985) report that *P. trigonatus* in amazonian forest habitat construct nests with the egg chamber next to an active termite mound. Metabolic heat from the termite mound incubates the eggs. If this strategy is used by *P. trigonatus* in southern Venezuela, it would explain the presence of this species at almost subtropical altitudes. The majority of the temperatures for *C. c. crocodilus* were measured at night when the bodies of water were cooling, whereas those for the other two crocodilians were measured during the day (see appendix). This probably biased downwards the temperatures for *C. c. crocodilus* habitat. The temperatures of standing water (lagoons and ponds) show greater diurnal variation when compared to rivers. The adjacent vegetation can also affect temperature, and small rivers in forests will be cooler than similar sized rivers in savannas at the same altitude. Therefore, altitude should not be regarded as the only factor that affects the water temperatures of crocodilian habitats.

Figure 2 shows the relationship between total cations and conductivity for the three crocodilian habitats and an additional 17 rivers from the Venezuelan Llanos and Venezuelan Guayana. Total cations are proportional to the conductivity ($r = 0.82$). It should be noted that, although all of the *P. trigonatus* habitats that were analyzed are rivers whereas most of the *Caiman* habitats are lagoons, the two *C. c. crocodilus* habitats that are flowing water (Yuruari and La Devuelta) fall well within the limnological range for the lagoon localities for that subspecies. Likewise, the values for two samples sites on the Apure river are within the upper range of the values for *C. crocodilus* (Llanos). It appears that the limnological differences are not a case of flowing versus standing water.

The majority of the data reported here were from samples taken during the rainy season from June to August. However, conductivity and cation concentrations in the Orinoco and Caroní rivers may increase by a factor of 2 during the dry season (Paolini et al. 1983). A similar effect is seen in two out of five Llanos lagoons (Table 2) sampled during February and June.

The grouping of the limnological characteristics of the habitats for the three crocodilians could be explained by the basic geology and geomorphology of the three study areas. The Gran Sabana is an area which drains off of an old erosion surface of Precambrian quartzites dominated by sandstone table-mountains which reach elevations of 2,800 m (Schubert et al. 1986). The waters which drains off of these table mountains are acidic and with a very low concentration of cations (Grupo Científico Chimanta 1986). The Venezuelan Llanos is an alluvial flood plain that receives nutrient rich waters from the Venezuelan Andes.

If the distributions of the three crocodilians were simply due to biogeography and if the limnological characteristics of their habitats have no direct ecological relationship, then one would not expect to find any one of these crocodilians outside of the defined geological areas. This, however, is not the case. *P. trigonatus* has been reported from the Llanos in the Rio Cinaruco (Godshalk 1982). This river (Figure 1) is exceptional in that its head waters are palm swamps within the Orinoco flood plain and that it does not receive waters from the Andes. The limnological characteristics of the Cinaruco are within those values that are characteristic of *P. trigonatus* habitats in the Gran Saban (Figure 2). Thus, two different geological and geomorphological situations have given rise to rivers with the same limnological characteristics and the same crocodilian is found in both. Within the lowlands of the Venezuelan Guayana both *C. c. crocodilus* and *P. trigonatus* occur over the same general geological area, and have also been occasionally found to occur sympatrically (Gorzula and Paolini 1986). In the latter situations it is not known whether this is a permanent or a seasonal phenomenon. This suggests that there is an ecological relationship between the limnological characteristics of the habitat and the crocodilian that occurs there.

Hydrology - Tables 3 and 4 show the individual, maximum and minimum elevations above sea level, catchment areas that drain down to the locality, annual rainfall, annual runoff, and estimated flowrates for *C. intermedius* and *P. trigonatus* habitats, respectively. Means and standard deviations are given for rainfall and runoff.

It can be seen that, apart from a single elevation of 300 m, the localities for *C. intermedius* are at very low elevations on the Orinoco floodplain, whereas *P. trigonatus* shows a wide altitudinal range from 50 - 1,340 m.

Catchment areas and estimated flowrates for the habitats of both species are somewhat inconclusive. Although it seems that *C. intermedius* occurs in "larger rivers", we do not have sufficient information to separate which localities represent resident breeding populations from those that are merely used partially or seasonally by individual crocodiles. In the case of *P. trigonatus* many (if not all) of the localities may be of "surplus" males, with the true populations being in side creeks. Studies in the Manaus area by Magnusson (pers. comm.) show that *P. trigonatus* inhabits small forest streams.

With regard to rainfall and runoff there seems to be a reasonable degree of separation with *C. intermedius* localities being in areas of somewhat lower rainfall and much lower runoff.

CONCLUSIONS

It is shown in this paper that *P. trigonatus*, *C. c. crocodilus* and *C. crocodilus* (Llanos) habitats may be differentiated on the basis of limnological characteristics, and that *P. trigonatus* and *C. intermedius* habitats may be separated on the basis of hydrological characteristics.

The limnological data presented in this paper may be gathered directly, quickly and economically in the field (water temperature, pH and conductivity), or obtained by the laboratory analyses of small easily obtainable water samples (Ca^{++} , Mg^{++} , Na^{+} , K^{+} and total cations). The hydrological data presented in this paper may be calculated and/or interpolated from existing maps and water resources data that, in Venezuela at least, are readily available. In the case of the hydrological data the principal limitation is the knowledge of the exact localities of the crocodilians, which greatly restricts the use of literature sources of locality information, because many authors give only imprecise data. The data are not vulnerable to uncontrolled subjective interpretations during collection and subsequent manipulation, and the information is scientifically defensible and repeatable. For this paper we were unable to assemble sufficient data with regard to the annual hydrological regime of the rivers under consideration, but on the basis of the general information that exists for the Llanos (Zinck 1977) we consider that this could be an essential parameter for riverine crocodilian species that are hole-nesters. Additional geomorphological and surface water

descriptors such as permanence, relief, grain, slope and drainage channel density for rivers and their valleys, and permanence, frequency and area for ponds, lagoons, lakes and swamp (Laut et al. 1977), which are also easily obtainable from existing thematic cartography, could also be applied in this type of study.

If, as it is suggested in this paper, these are real correlations between limnological and hydrological characteristics of both channeled and enclosed bodies of water and the crocodilian species that inhabit them, a system of classifying crocodilian habitats based on limnology and hydrology would have several applications in management and conservation:

- 1) Hydrological and relevant geomorphological data could be gathered and processed prior to surveying, and used to establish the areas that should be given priority.
- 2) Censuses could relate densities to measurable physical and chemical parameters, which in turn may help in explaining differences in population dynamics, carrying capacity, etc.
- 3) In the case of plans for reintroducing a species into areas where it is assumed to have occurred previously the optimum sites could be more easily selected.
- 4) A concise knowledge of the limnological and hydrological requirements of crocodilian species would enable environmental impact assessments of large scale water resource projects, such as dams and canalizations, to be made.

ACKNOWLEDGEMENTS

We wish to express our thanks to Tomás Blohm, Chucho Regetti and Robert Sentell for their assistance with providing field facilities in Hato Masaguaral, Hato Terecay and El Manteco respectively. Luis Castro, Margarita de Guell and Horst Folster made valuable comments on the hydrological and limnological aspects of this work. We also acknowledge the technical assistance of Mr. Saúl Flores of the IVIC Laboratory in Caracas. EDELCA gave financial support and encouragement for Gorzula to attend the conference. This paper is, in part, an incidental result of an ecosystem inventory being carried out by EDELCA in the Caroni River Basin.

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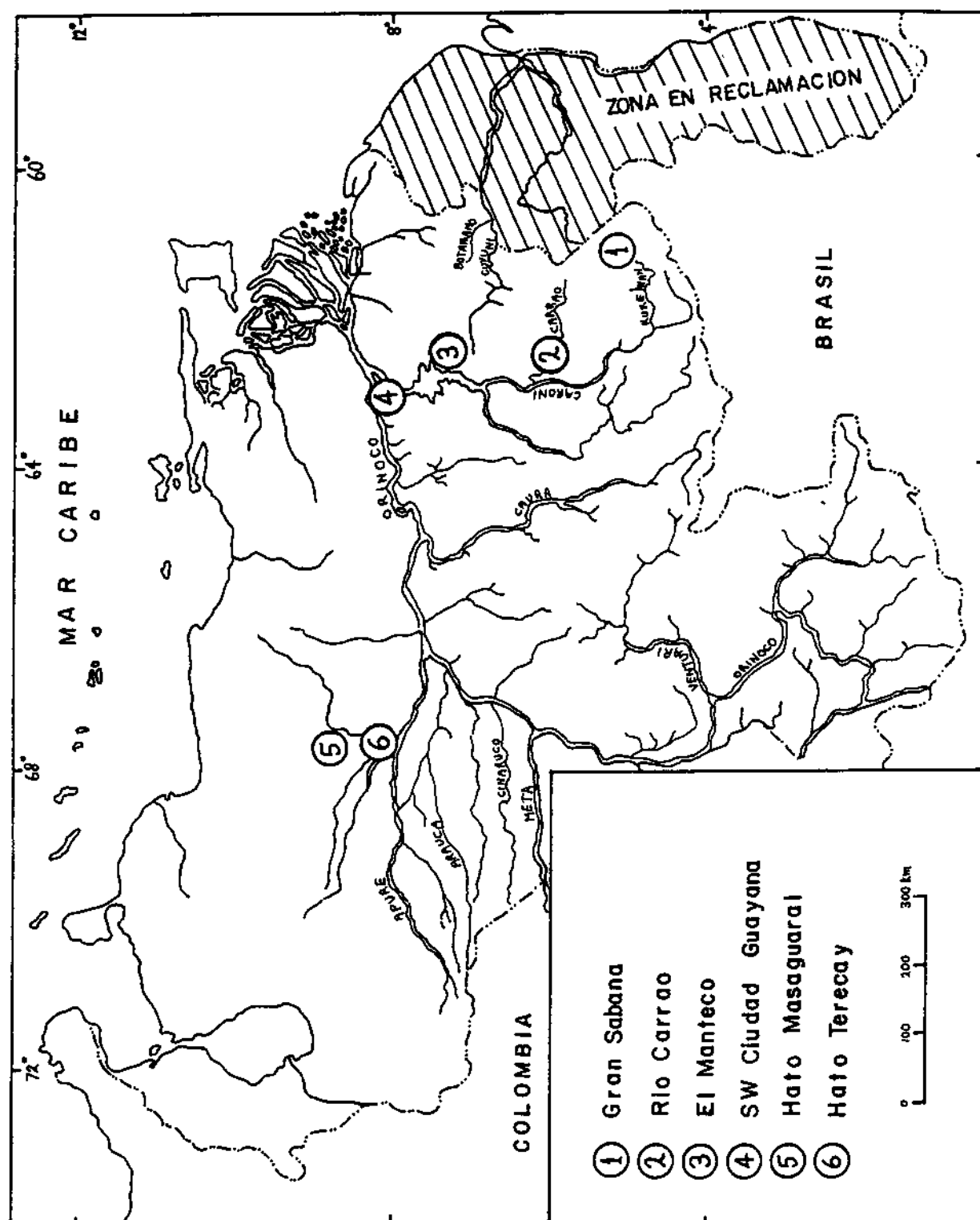


Figure 1. Map of Venezuela showing the 6 principal areas where limnological data was gathered for *Paleosuchus trigonatus* (1 and 2), *Caiman crocodilus crocodilus* (3 and 4), and *Caiman crocodilus* (Llanos) (5 and 6).

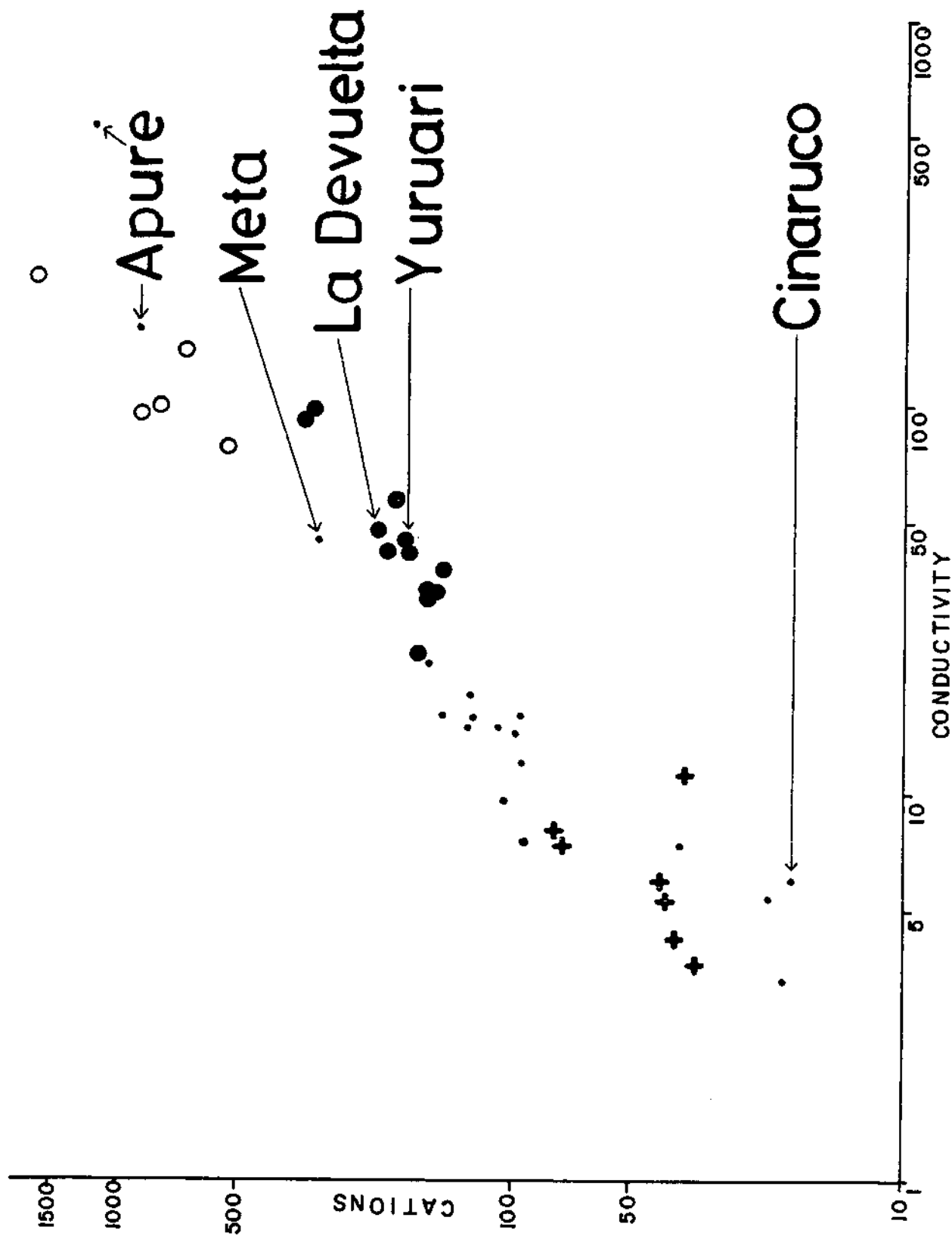


Figure 2. Plot total cations (Ueg/l) against conductivity (MHOS) for *Paleosuchus trigonatus* (crosses), *Caiman crocodilus crocodilus* (closed circles), and *Caiman crocodilus* (Llanos) (open circles), and a series of Venezuelan rivers (dots).

Table 1. Physio-chemical parameters of the aquatic habitats of *Paleosuchus trigonatus*, *Caiman crocodilus crocodilus* and *Caiman crocodilus* (Llanos). The mean values with their standard deviations in parenthesis are shown, except for pH where the maximum and minimum values are given.

| | <i>Paleosuchus trigonatus</i> | <i>Caiman crocodilus crocodilus</i> | <i>Caiman crocodilus</i> (Llanos) |
|-----------------------|-----------------------------------|---|--|
| Water temperature (C) | 22.4 (0.34) | 29.1 (2.69) | 32.4 (1.51) |
| pH | 4.2 - 6.7 | 5.2 - 7.0 | 5.7 - 9.3 |
| Conductivity (MHOS) | 6.6 (2.0) | 48.5 (13.3) | 125.6 (54.9) |
| Total cations (ueq/l) | 49.3 (19.2) | 215.8 (77.8) | 1,052.2 (735.1) |
| Ca++ (ppm) | 0.26 (0.12) | 1.16 (1.05) | 9.73 (10.56) |
| Mg++ (ppm) | 0.07 (0.05) | 0.55 (0.31) | 2.96 (1.56) |
| Na+ (ppm) | 0.41 (0.34) | 1.89 (0.96) | 16.07 (17.13) |
| K+ (ppm) | 0.48 (0.23) | 1.17 (0.83) | 4.25 (2.08) |
| Number of samples | 7 | 15 | 7 |

Table 2. Changes between dry season (FEB) and wet season (JUN) in pH and conductivity (COND) in lagoons inhabited by *Caiman crocodilus* (Llanos) in Hato Masaguaral, Estado Guarico, Venezuela. The sampling dates (DATES) and hours (TIME) are shown along with water temperatures (WATER) and air temperatures (AIR) in C.

| Lagoon | Date | Time | Water | Air | pH | Cond. |
|--------------|-------------|------|-------|------|-----|-------|
| Prestamo #09 | 22 FEB 1986 | 1725 | 28.0 | 33.0 | 6.6 | 135 |
| | 14 JUN 1986 | 1436 | 31.0 | 32.4 | 6.8 | 95 |
| Prestamo #14 | 22 FEB 1986 | 1755 | 29.0 | 32.5 | 9.3 | 264 |
| | 14 JUN 1986 | 1420 | 32.0 | 32.4 | 9.3 | 215 |
| Prestamo #19 | 22 FEB 1986 | 1810 | 28.0 | 32.0 | 9.0 | 271 |
| | 14 JUN 1986 | 1405 | 31.0 | 30.3 | 6.6 | 100 |
| Alta Vanega | 22 FEB 1986 | 1903 | 28.0 | 30.0 | 6.1 | 65 |
| | 14 JUN 1986 | 1459 | 34.0 | 33.2 | 6.1 | 78 |
| El Guacimo | 22 FEB 1986 | 1235 | 27.0 | 28.0 | 6.1 | 93 |
| | 14 JUN 1986 | 1539 | 34.0 | 33.0 | 6.6 | 140 |

Table 3. Hydrological characteristics of rivers with *Crocodylus intermedius*, giving the name of the locality (LOCALITY), geographical coordinates (COORDINATES), elevation above sea level in meters (ELEV.), catchment area that drains to the locality (CATCHMENT), mean annual rainfall (mm) in the catchment area (RAIN), mean annual runoff (mm) in the catchment area (RUNOFF), and the estimated flowrate (m³/s) of the river at the locality (FLOW).

| Locality | Coordinates | Elev. | Catchment | Rain | Runoff | Flow |
|--------------|---------------------|-------|-----------|-------|--------|--------|
| Orinoco 1 | 0624N-6711W | 40 | --- | --- | --- | --- |
| Orinoco 2 | 0837N-6214W | 5 | 1,123,000 | 2,550 | 926 | 33,000 |
| Orinoco 3 | 0755N-6434W | 10 | --- | --- | --- | --- |
| Caura 1 | 0737N-6453W | 10 | 48,100 | 2,950 | 1,800 | 2,745 |
| Caura 2 | 0623N-6436W | 150 | 28,435 | 2,950 | 2,040 | 1,840 |
| Cuchivero | 0720N-6549W | 35 | 14,520 | 2,440 | 1,135 | 520 |
| Guaniamo | 0704N-6547W | 35 | 6,350 | 2,440 | 1,135 | 230 |
| Ventuari | 0415N-6625W | 100 | 34,030 | 3,150 | 1,745 | 1,180 |
| Cinaruco 1 | 0634N-6845W | 70 | 3,930 | 1,950 | 405 | 50 |
| Cinaruco 2 | 0632N-6814W | 60 | 5,445 | 1,950 | 405 | 70 |
| Capanaparo 1 | 0656N-6720W | 40 | 17,700 | 1,800 | 185 | 105 |
| Capanaparo 2 | 0656N-6807W | 50 | 14,820 | 1,800 | 185 | 90 |
| Arauca | 0702N-7110W | 125 | --- | 1,900 | 460 | --- |
| Apure | 0800N-6811W | 45 | 53,240 | 2,200 | 780 | 1,320 |
| Manapire | 0751N-6611W | 40 | 7,260 | 1,300 | 100 | 23 |
| Rabanal | 0819N-6710W | 45 | 18,450 | 1,100 | 300 | 175 |
| Guarico | 0856N-6724W | 105 | 7,865 | 1,100 | 300 | 75 |
| Camatagua | 0948N-6654W | 300 | 1,815 | 1,100 | 300 | 17 |
| Chirgua | 0856N-6755W | 70 | 3,025 | 1,150 | 510 | 50 |
| Portuguesa | 0815N-6738W | 55 | 52,030 | 1,300 | 510 | 840 |
| Guanare | 0820N-6808W | 40 | 6,960 | 1,600 | 1,035 | 230 |
| Cojedes | 0900N-6825W | 60 | 7,865 | 1,200 | 510 | 130 |
| Camoruco | 0922N-6845W | 110 | 605 | 1,200 | 510 | 10 |
| Tucupido | 0857N-6950W | 135 | 393 | 1,700 | 1,035 | 13 |
| Boconó | 0847N-6952W | 130 | 1,695 | 1,700 | 1,035 | 55 |
| Tinaco | 0926N-6825W | 100 | 1,240 | 1,200 | 510 | 20 |
| San Carlos | 0920N-6833W | 105 | 1,996 | 1,200 | 510 | 32 |
| | MAXIMUM: | 300 | 1,123,000 | 3,150 | 2,040 | 33,000 |
| | MINIMUM: | 5 | 393 | 1,100 | 100 | 10 |
| | MEAN: | --- | --- | 1,797 | 734 | --- |
| | STANDARD DEVIATION: | --- | --- | 644 | 526 | --- |

Table 4. Hydrological characteristics of rivers with *Paleosuchus trigonatus*, giving the name of the locality (LOCALITY), geographical coordinates (COORDINATES), elevation above sea level in meters (ELEV.), catchment area that drains to the locality (CATCHMENT), mean annual rainfall (mm) in the catchment area (RAIN), mean annual runoff (mm) in the catchment area (RUNOFF), and the estimated flowrate (m³/s) of the river at the locality (FLOW).

| Locality | Coordinates | Elev. | Catchment | Rain | Runoff | Flow |
|-------------|---------------------|-------|-----------|-------|--------|------|
| Cinaruco | ??-?? | 50 | 17,700 | 1,800 | 185 | 105 |
| Uruyen | 0542N-6226W | 480 | 155 | 2,400 | 1,660 | 8 |
| Cuyuni | 0643N-6105W | 110 | 31,160 | 2,000 | 750 | 740 |
| Botanamo | 0652N-6052W | 100 | 7,560 | 1,600 | 750 | 180 |
| La Escalera | 0554N-6125W | 1,340 | 5 | 3,200 | 1,660 | 0.25 |
| Carrao | 0614N-6247W | 450 | 7,585 | 2,500 | 1,660 | 400 |
| Kukenan 1 | 0455N-6123W | 820 | 5,060 | 2,000 | 1,610 | 260 |
| Kukenan 2 | 0455N-6112W | 830 | 3,015 | 2,000 | 1,610 | 155 |
| Yuruani 1 | 0458N-6115W | 830 | 1,480 | 2,000 | 1,610 | 75 |
| Yuruani 2 | 0503N-6107W | 840 | 1,240 | 2,000 | 1,610 | 65 |
| Jaspe | 0456N-6106W | 940 | 21 | 1,850 | 1,610 | 1.1 |
| Yureba | 0403N-6601W | 130 | 38 | 2,800 | 1,680 | 2 |
| Puruname | 0325N-6618W | 100 | 1,930 | 3,300 | 1,610 | 100 |
| Baria | 0105N-6625W | 150 | 1,285 | 3,000 | 1,720 | 70 |
| Mawarinuma | 0050N-6612W | 150 | 245 | 3,000 | 1,720 | 13 |
| Yagua | 0332N-6646W | 120 | 2,955 | 3,300 | 1,610 | 150 |
| | MAXIMUM: | 1,340 | 31,160 | 3,300 | 1,720 | 740 |
| | MINIMUM: | 100 | 5 | 1,600 | 185 | 0.25 |
| | MEAN: | --- | --- | 2,422 | 1,441 | --- |
| | STANDARD DEVIATION: | --- | --- | 591 | 453 | --- |

APPENDIX

Raw Data for Localities and Physico-chemical Parameters Used in This Paper.

[Name of locality: geographic coordinates; elevation above sea level in meters; date; hour sample taken; air temperature (°C); water temperature (°C); pH; conductivity (MHOS); total cations in ueq/l; Calcium (Ca++) in ppm; Magnesium (Mg++) in ppm; Sodium (Na+) in ppm; Potassium (K+) in ppm. For *Caiman crocodilus crocodilus* those lagoons that were letter coded in Gorzula (1978) have the corresponding code indicated in parenthesis.]

Paleosuchus trigonatus:

RIO YURUANI: 05057N-6140W; 870m; 08 AUG 1985; ?? hours; air ??; water 23.0; pH 5.7; conductivity 3.7; cations 34.4; Ca++ 0.11; Mg++ 0.03; Na+ 0.39; K+ 0.37. RIO YURUANI: 0507N- 6104W; 870m; 04 AUG 1984; 1745 hours; air 21.7; water 22.5; pH 5.8; conductivity 4.1; cations 37.9; Ca++ 0.37; Mg++ 0.16; Na+ 0.16; K+ 0.32. QUEBRADA DE JASPE: 0455N-6106W; 940m; 04 AUG 1984; 1515 hours; air 23.3; water 22.2; pH 6.1; conductivity 6.0; cations 41.9; Ca++ 0.38; Mg++ 0.06; Na++ 0.19; K+ 0.37. QUEBRADA DE JASPE: 0455N-6106W; 940m; 08 AUG 1985; ?? hours; air ??; water 22.5; pH 6.7; conductivity 7.6; cations 76.8; Ca++ 0.23; Mg++ 0.14; Na+ 0.75; K+ 0.83. RIO CARRAO: 0615N-6249W; 450m; 01 SEP 1984; 1000 hours; air ??; water 22.7; pH 4.2; conductivity 11.5; cations 36.0; Ca++ 0.12; Mg++ 0.14; Na+ 0.23; K+ 0.33. RIO KUKENAN: 0455N-6612W; 830m; 04 AUG 1984; 0950 hours; air 23.6; water 22.2; pH 5.2; conductivity 5.3; cations 40.5; Ca++ 0.39; Mg++ 0.08; Na+ 0.15; K+ 0.32. RIO URUYEN: 0542N-6226W; 480m; 16 JAN 1986; 0920 hours; air 26.0; water 22.0; pH 6.2; conductivity 8.0; cations 77.3; Ca++ 0.22; Mg++ 0.01; Na+ 1.03; K+ 0.81.

Caiman crocodilus crocodilus:

KM 15 SOUTH EL MANTECO: 0714N-623W; 290m; 05 AUG 1985; 2004 hours; air 25.0; water 28.0 pH 6.5; conductivity ??; cations 122.8 Ca++ 0.72; Mg++ 0.29; Na+ 0.45; K+ 1.70. CANAOTALES (LAGOON "T"): 0721N-6231W; 280m; 31 JUL 1984; 2150 hours; air 26.0; water 28.0; pH 6.3 conductivity 38.0 cations 151.7; Ca++ 0.69; Mg++ 0.60; Na+ 1.25; K+ 0.53. EL MURO: 0720N-6229W; 260m; 31 JUL 1984; 1800 hours; air 27.0; water 33.0; pH 5.2; conductivity 33.0; cations 156.0; Ca++ 0.41; Mg++ 0.54; Na+ 1.86; K+ 0.40. EL PILON (LAGOON "J"): 0721N- 6231W; 280m, 31 JUL 1984; 2115 hours; air 24.0; water 29.5; pH 6.0; conductivity 33.0; cations 161.6; Ca++ 0.74; Mg++ 0.92; Na+ 0.89; K+ 0.40. LA ATARAYA: 0717N-6228W; 280m; 31 JUL 1984; 1705 hours; air 26.5; water 34.0; pH 7.0; conductivity 31.5; cations 166.8; Ca++ 0.45; Mg++ 0.23; Na+ 2.56; K+ 0.55. EL ZAMURO: 0719N-6228W; 260m; 31 JUL 1984; 1730 hours; air 26.5; water 33.0; pH 5.9; conductivity 23.1; cations 170.9; Ca++ 0.34; Mg++ 0.06; Na+ 2.28; K+ 1.95. RAJA IZQUIERDA (LAGOON "F"): 0722N-6230W; 280m; 31 JUL 1984; 2220 hours; air 23.5; water 27.7; pH 5.8; conductivity 42.0; cations 184.5; Ca++ 0.41; Mg++ 0.20; Na 3.17; K+ 0.38. RIO YURUARI: 0720N-6229W; 260m; 31 JUL 1984; 1745 hours; air 27.5; water 24.5; pH 6.5 conductivity 45.5; cations 190.1; Ca++ 0.72; Mg++ 0.74; Na+ 1.78; K+ 0.62. LAPA MATA (LAGOON "E"): 0721N-6231W; 280m; 31 JUL 1984; 2130 hours; air 23.5; water 28.5; pH 5.8; conductivity 57.0; cations 198.2; Ca++ 0.55; Mg++ 0.50; Na+ 2.44; K+ 0.92. RAJA (LAGOON "F"): 0722N-6230W; 280m; 31 JUL 1984; 2205 hours; air 24.0; water 28.0; pH 5.6; conductivity 42.0; cations 212.5; Ca++ 0.42; Mg++ 0.18; Na+ 3.70; K+ 0.62. LA DEVUELTA: 0720N-6231W; 260m; 31 JUL 1984; 1820 hours; air 23.5; water 26.0; pH 6.2; conductivity 47.5; cations 222.9; Ca++ 0.93; Mg++ 0.82; Na+ 2.23; K+ 0.47. CALCETA LARGA: 0717N-6234W; 250m; 03 AUG 1985;

2038 hours; air 24.0; water 31.0; pH 7.0; conductivity ??; cations 245.5; Ca++ 2.21; Mg++ 0.48; Na+ 1.06; K+ 1.94. 4 KM SUR KM 70: 0808N-6257W; 100m; 11 JAN 1986; 1430 hours; air ??; water 30.0; pH 6.5; conductivity 98.0; cations 321.2; Ca++ 2.16; Mg++ 0.81; Na+ 2.07; K+ 2.22. 5 KM SUR KM 70: 0808N-6257W; 100m; 11 JAN 1986; 1445 hours; air ??; water 27.0 pH 6.1; conductivity 92.0; cations 337.8; Ca++ 3.44; 1.03 Mg++; Na+ 0.29; K+ 2.69. RIO YURUARI: 0720N- 6229W; 260m; 02 JUN 1985; 1612 hours; air ??; water 28.0; pH 6.9; conductivity ??; cations 395.3; Ca++ 3.19; Mg++ 0.92; Na+ 2.39; K+ 2.21.

Caiman crocodilus (Llanos):

MASAGUARAL ALTA VANEGAS: 0840N-6838W; 75m; 14 JUN 1986; 1459 hours; air 33.2; water 34.0; pH 6.1; conductivity 78.0; cations 537.1; Ca++ 1.64; Mg++ 0.72; Na+ 4.36; K+ 8.07. MASAGUARAL EL GUACIMO: 0840N-6838W; 75m; 14 JUN 1986; 1539 hours; air 33.0; water 34.0; pH 6.6; conductivity 140.0; cations 690.7; Ca++ 2.23; Mg++ 1.91; Na+ 7.14; K+ 4.37. PALMA MOROCHA PRESTAMO 19: 0840N-6838W; 75m; 14 JUN 1986; 1405 hours; air 30.3; water 31.0; pH 6.6; conductivity 100.0 cations 788.4; Ca++ 3.59; Mg++ 3.27; Na+ 5.90; K+ 3.27. PALMA MOROCHA PRESTAMO 09: 0840N-6838W; 75m; 14 JUN 1986; 1436 hours; air 32.4; water 31.0; pH 6.8; conductivity 95.0; cations 881.2; Ca++ 3.30; Mg++ 3.54; Na+ 7.49; K+ 3.89. PALMA MOROCHA PRESTAMO 14: 0840N-6838W; 75m; 14 JUN 1986; 1420 hours; air 32.4; water 32.0; pH 9.3; conductivity 215.0; cations 1,640.0; Ca++ 7.50; Mg++ 4.48; Na+ 18.85; K+ 3.03. HATO TEREAY 01: 0800N-6736W; 65m; 20 MAY 1985; 1555 hours; air ??; water 34.0; pH 7.3; conductivity ??; cations 2,448.4; Ca++ 23.69; Mg++ 5.31; Na+ 15.82; K+ 5.53. HATO TEREAY 02: 0800N-6836W; 65m; 19 MAY 1985; 1100 hours; air ??; water 31.0; pH 5.7; conductivity ??; cations 3,769.4; Ca++ 26.15; Mg++ 1.50; Na+ 52.92; K+ 1.57.

CROCODILIAN UTILIZATION AND PUBLIC EDUCATION: DIFFICULTIES IN EXPLAINING CONSERVATION

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Until recently, the commercial utilization of crocodilian skins was met exclusively by hunting wild crocodilians. The decline in wild populations due to over-hunting and habitat destruction alerted conservationists throughout the globe. They campaigned against the use of crocodilian products. Politically active conservation organizations succeeded nationally in setting up sound conservation laws. On an international front CITES was set up in 1975, thus bringing to halt almost all trade in Appendix I species between party nations and somewhat controlling the trade volume of Appendix II species.

The worldwide demand for the classical crocodile skins, such as *Crocodylus niloticus* and *Crocodylus porosus* shifted to *Caiman* skins and pressed different agencies to define the term 'captive bred' to CITES at the San Jose meeting in 1979.

At the Delhi meeting of CITES parties in 1981 the term 'ranching' was introduced, whereby populations of species in Appendix I which would benefit from ranching could be transferred to Appendix II. Ranching is defined as the rearing in a controlled environment of specimens taken from the wild, for the purpose of the trade. The ranching scheme must be beneficial to the wild populations and the products must be marked to be easily distinguished from products of other populations of the same species in Appendix I.

At the Buenos Aires meeting of CITES parties in 1985, another more liberal measure for trade in crocodilian products was introduced. This was the setting of quotas for each country wishing to trade in a species, in conjunction with an approved management plan.

Besides crocodilian products from ranching enterprises and from the quota system, there are now skins (e.g., *Alligator mississippiensis*) available from harvesting systems. Compared to the earlier figures of the hide trade, the number of crocodilian skins originating from legal sources is still relatively small, but the trend is increasing.

The question is open to debate. Should we as conservationists support this increasing trend or should we still work against commercial utilization of all crocodilian products - i.e., campaign against the use of crocodilian skins in the fashion trade? Looking at this eminent query we must keep in mind that there is an ecological and an economic aspect to it.

On the ecological side it is known that crocodilians are an important part (foodchains, species diversification, habitat forming) within all ecosystems they originally live in. This influence remains true for all artificial operations - captive breeding and/or farming for genetic enhancement - and harvesting systems. Crocodilian farming does not require forest cleaning, planting or alien plants and the use of biocides. The intimately associated economic aspect is the crucial point: without considering it, all our efforts to save crocodilians from becoming extinct will be in vain. We no longer can depend merely on the goodwill of the people living in the tropics among crocodilians to understand our ethical efforts 'to save crocodilians', but we must accept their willingness to utilise crocodilians as a source of their regular income, similar to their revenue from wetland fisheries, crabfishing, hunting and plant harvesting. Hopefully the Convention on

Wetlands of International importance (Ramsar Convention) with 40 contracting state parties will provide such benefits not only through fishery and timber production, but also from crocodilian harvesting.

Crocodilian exploitation under sound management criteria or under international control, such as provided by CITES for quotas can reduce economic pressure for wetland reclamation. This will assist in the conservation of other species.

All legal crocodilian exploitation is overshadowed by widespread and well organized poaching and smuggling of products. The efforts to internationally control such developments must become enforced (CITES). Despite that last fact, I consider it essential for the survival of all crocodilians throughout the globe that their products should be traded within strict national and international limits and controls.

To return to the title question: How do we answer the consumer question about the trading of 'endangered crocodilians' without bias? Naively, I could say by availing ourselves of an excellent opportunity for a close cooperation between the conservationists and the traders, perhaps in the beginning with the mediation of conservation agencies.

AN OVERVIEW OF CROCODILE MANAGEMENT IN AUSTRALIA 1985-86, WITH PARTICULAR REFERENCE TO THE NORTHERN TERRITORY

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This paper summarizes the progress made in crocodilian management within Australia during the period 1985-86. It deals with both the Australian freshwater crocodile, *Crocodylus johnstoni*, and the estuarine crocodile, *Crocodylus porosus*. Both species are found within the three northern States of Australia (Western Australia, Queensland and the Northern Territory), where their management is the responsibility of the respective State Wildlife Services. A Federal Wildlife Service (Australian National Parks and Wildlife Service - ANPWS) is responsible for crocodile management within Federal National Parks (including Kakadu National Park in the Alligator Rivers region of the Northern Territory). ANPWS is also the designated authority under CITES and is responsible for regulating the import and export of crocodiles, or products derived from them.

Australian policy on matters to do with crocodiles and other wildlife is coordinated by the Council of Nature Conservation Ministers (CONCOM), and its supporting committees, which include representatives from all Wildlife Services within Australia.

CITES LISTING OF CROCODILES IN AUSTRALIA

Crocodylus johnstoni is listed on Appendix II of CITES. The Australian population of *C. porosus* was on Appendix II until 1979, when the world population was shifted to Appendix I (with the exception of the population being utilized in Papua New Guinea). The detailed proposal to have the Australian population of *C. porosus* replaced on Appendix II for the purposes of management (Webb et al. 1984) was strongly supported by the SSC Crocodile Specialists Group, the IUCN General Assembly and finally by the members attending the 1985 meeting of the parties to CITES in Buenos Aires. The Australian population has now been replaced on Appendix II, and appropriate amendments have been made to the scheduling of *C. porosus* within the Federal legislation. Australia has complied with the requirements of Resolution 5.16 of CITES regarding trade in ranched products and the intended methods of product identification have been approved.

APPROVED MANAGEMENT PROGRAMS

Under the Australian Wildlife Protection (Regulation of Exports and Imports) Act 1982, the export for commercial purposes of products derived from wild crocodilians and other native wildlife is subject to detailed management programs being formulated by State Authorities and approved at the Federal level. Permits, but not approved management programs, are required for the commercial export of products derived from captive bred animals. Management programs for both *C. johnstoni* and *C. porosus* within the Northern Territory have been refined during the 1984-86 period and have now been submitted by the Northern Territory Minister for Conservation to the Federal Minister for Arts, Heritage and the Environment (September 1986).

CROCODILE MANAGEMENT CONFERENCE

Under the auspices of CONCOM and the Conservation Commission of the Northern Territory, an internationally attended conference on crocodilian management was held in Darwin, on 13-18 January 1985. Participants came from eleven countries (Australia (74); India (3); Israel (1); Papua New Guinea (4); South Africa (1); Thailand (3); United States of America (5); United Kingdom (2); Venezuela (2); Zambia (1); Zimbabwe (5)) and presented fifty-one papers. The emphasis of the conference was on the ways in which crocodilian populations can and are being successfully managed in different parts of the world - the techniques which have been developed, the problems that have been encountered and overcome and the research advances that have been made, particularly in reproductive biology, embryology, monitoring methods, population modelling and crocodilian farming.

The conference allowed full and open debate of both the background research incorporated into the successful Australian submission to CITES and the management programs being developed for both *C. porosus* and *C. johnstoni* within the Northern Territory. It also allowed international participants to see the wild populations of *C. porosus* in both tidal and freshwater swamp habitats, and to participate in some aspects of the *C. porosus* nesting research in freshwater swamps.

The proceedings of the conference are to be published (late 1986) in a hard-bound book entitled: "Wildlife Management: Crocodiles and Alligators." It contains 51 chapters subdivided into ten parts, each of which deals with a specific aspect of crocodilian conservation and management [Part I, World Crocodilians; Part II, Crocodilian Management Programs; Part III, Crocodile Management and Indigenous People; Part IV, Studying Crocodilian Populations; Part V, Public Education; Part VI, Capturing Crocodilians; Part VII, Understanding Crocodilian Behavior and Temperature Regulation; Part VIII, "Farming" Crocodilians; Part IX, Crocodilian Skins; Part X, Understanding Crocodilian Eggs and Embryos]. It is hoped that the compendium of crocodilian management information contained within the book will be of assistance to people attempting to manage wild crocodilian populations throughout the world.

FATALITIES

C. porosus have been responsible for two severe maulings and three fatalities in Australia during 1985-86. Such attacks highlight the public safety factor involved with *C. porosus* conservation and management in northern Australia. Unless the public perception of the wild *C. porosus* populations is enhanced in synchrony with their increasing numbers, such attacks represent a very real threat to the existence of high densities of the species in the wild. Public safety and public education about crocodiles are essential requisites of crocodile management programs in northern Australia.

If minor incidents are ignored, there have now been seven fatal and three near-fatal attacks caused by *C. porosus* in Northern Australia since protection (Fig. 1); one in Western Australia, six in the Northern Territory and three in Queensland. Of these ten, seven involved people swimming in areas that contain *C. porosus* (the others occurred when people were washing beside a billabong, wading on the edge of a swamp and canoeing). Five of the attacks involved people who were locals and the other five were either tourists or recent residents from other parts of Australia. Seven of the attacks resulted from voluntary actions which were unnecessary, whereas three arose in the course of necessary work activities. Alcohol consumption prior to the attack, which may have dampened normal caution, was involved in four of the ten attacks.

Fatalities caused by crocodiles are tragic and represent a real threat to public tolerance of high densities of wild crocodiles. However, they invariably result in Australia-wide media coverage about crocodiles and their conservation, which is a positive side-effect. Hundreds of thousands of tourists from

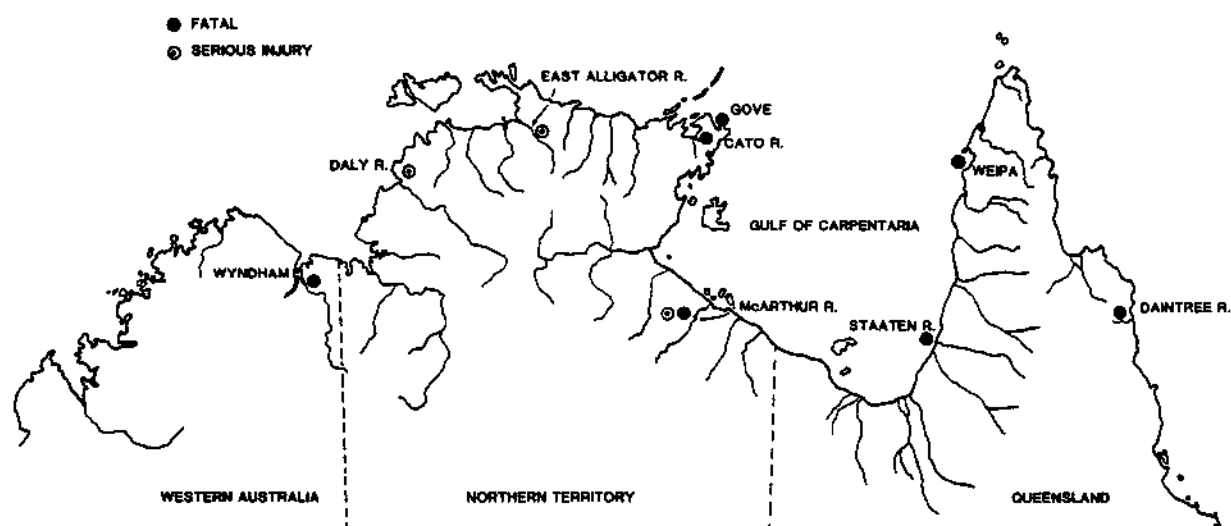


Figure 1. The locations where serious attacks by *C. porosus* on people have occurred since protection (in 1969-74).

the southern States visit the north annually, and such media attention creates "crocodile awareness" among them.

CROCODILE FARMING

The Edward River Crocodile Farm in North Queensland is now exporting skins, and the three farms within the Northern Territory are expected to begin exporting by the end of 1986. Husbandry research has continued to improve hatchling survival with *C. porosus*, and at least 80% survival from hatching to slaughter is now attainable. The approximate number of crocodiles maintained in captivity within each State in Australia is summarized in Table 1; the total captive population is some 19,220 crocodiles.

Table 1. The approximate numbers of crocodiles currently maintained in captivity within the three northern States of Australia.

| State | <i>C. porosus</i> | <i>C. johnstoni</i> | Totals |
|--------------------|-------------------|---------------------|---------------|
| Western Australia | 36 | 13 | 49 |
| Northern Territory | 4,232 | 8,593 | 12,825 |
| Queensland | 5,876 | 470 | 6,346 |
| TOTALS | 10,144 | 9,076 | 19,220 |

HIGHLIGHTS OF THE CROCODILE MANAGEMENT PROGRAM IN THE NORTHERN TERRITORY

1. Management Programs

Formal management programs for *C. porosus* (CCNT 1986a) and *C. johnstoni* (CCNT 1986c) within the Northern Territory have been submitted, and additional supporting information on the biology and history of management for both species has been prepared (CCNT 1986b, d). As outlined elsewhere (Webb et al. 1984, 1987), both programs make provision for ranching, based on the collection of eggs (*C. johnstoni* and *C. porosus*) and hatchlings (only *C. johnstoni*), followed by incubation and raising within three commercial crocodile farms.

2. Public Education

The public education program within the Northern Territory has continued with the aid of brochures, posters, a television advertisement, school talks by rangers, an educational slide kit and "no-swimming" signs which feature a crocodile. The metal signs and a miniaturized version made into a "sticker", can both be purchased by the public as souvenirs. A high profile media interest in crocodiles has been encouraged

as a means of disseminating information about crocodiles nationally. A recent one hour documentary entitled "Living with Crocodiles" was produced as part of the public education program. It is made available to schools, clubs and isolated communities.

As is often the case with dangerous animals, media attention reaches a peak when there are serious interactions between *C. porosus* and people. Public response in the Territory to three serious attacks on people during 1985-86 (including 1 fatality) has been both calm and rational.

3. Public Safety

Within the Northern Territory, "problem" crocodiles are broadly defined as:

1. Crocodiles within settled areas or areas of priority recreational use where that recreation is inconsistent with the risks associated with having *C. porosus* present; and,
2. Animals which are attacking stock in pastoral areas (CCNT 1986a).

During the period July 1984 to June 1986, 71 problem animals were removed from the wild and relocated into the crocodile farms. Of these, 57 came from Darwin harbour, making a total of 354 removed from there since protection and a total of 451 removed from the wild throughout the Northern Territory since protection.

4. Harvests from the Wild

During 1985, 1335 *C. johnstoni* eggs were harvested from the wild within the management areas defined in the Management Program (CCNT 1986c). The harvest was carried out by crocodile farmers under the supervision of the Conservation Commission of the Northern Territory (CCNT). Management areas were surveyed before (1985) and after (1986) the harvests.

Collections of wild *C. porosus* eggs have been restricted to research exercises carried out by CCNT staff and consultants within 140 km of Darwin. In the 1984/85 season, 3517 eggs were harvested and in the 1985/86 season 3470 eggs were harvested. The areas harvested have been surveyed by spotlight annually, and preliminary analyses indicate the impact on wild populations is negligible (see Webb et al. [this volume] for details).

5. Crocodile Farms

There are three crocodile farms within the Northern Territory. As of 30 June 1986, Crocodile Farms N.T. Pty. Limited contained 2830 *C. porosus* and 3274 *C. johnstoni*. During the 1984/85 and 1985/86 nesting seasons, 29 and 27 *C. porosus* nests were made on the farm. *Crocodylus johnstoni* nesting in captivity increased from 15 nests in 1985 to 32 in 1986. The other two farms are currently building facilities to house *C. porosus* breeding stock, which should begin breeding by the 1987/88 season. Stocks at Letaba Crocodile Farm on 30 June 1986 were 999 *C. porosus* and 3407 *C. johnstoni*. At Janamba Crocodile Farm stocks were 394 *C. porosus* and 1904 *C. johnstoni*. Three additional *C. porosus* nests are made annually in captivity each season at zoos, which contain an additional 9 *C. porosus* and 8 *C. johnstoni*.

No skins or other crocodile products have yet been sold from the farms, and they are currently stocked to capacity with problem crocodiles. Skin sales will begin following approval of the management programs in late 1986.

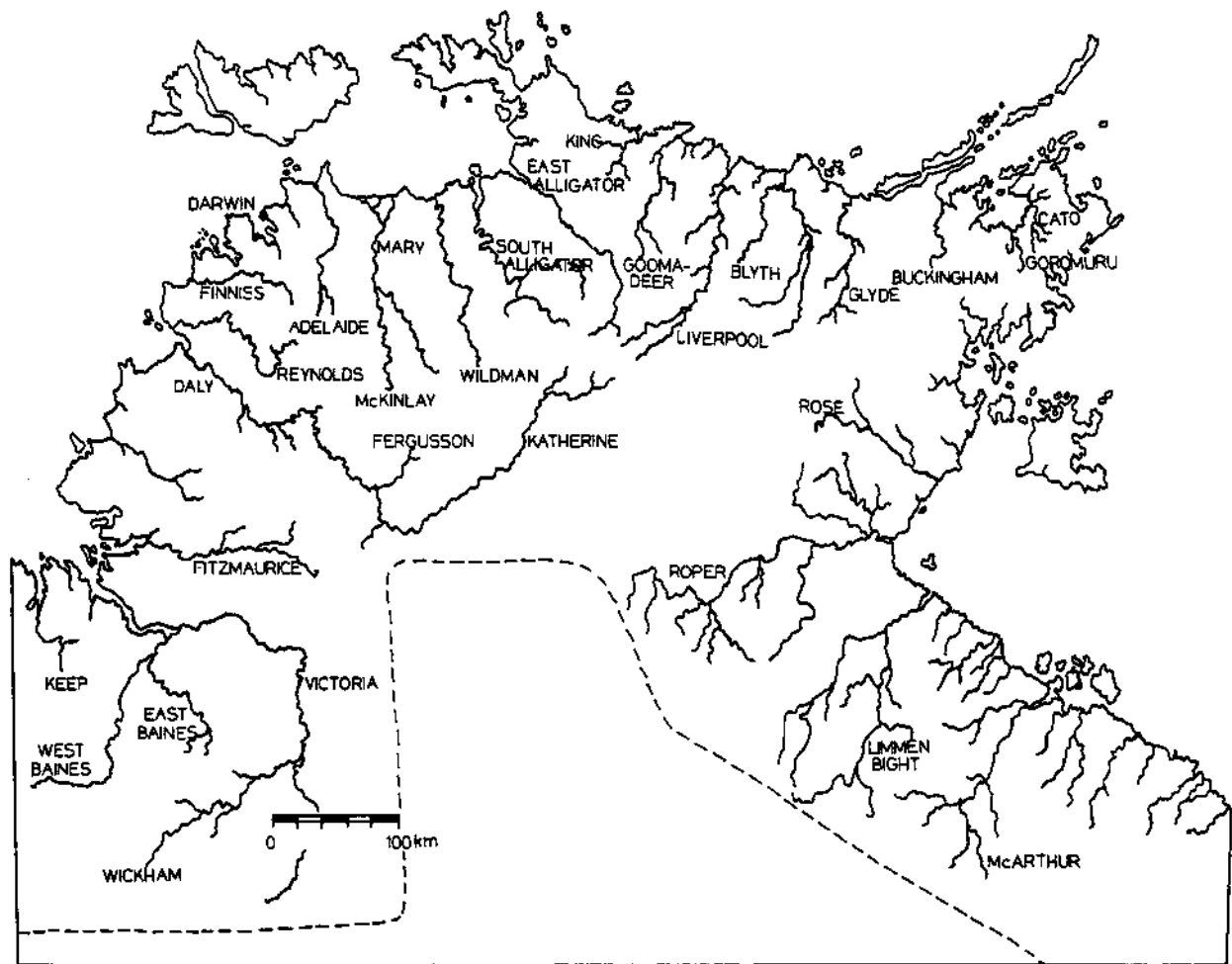


Figure 2. Locations of some of the major river systems within the Northern Territory.

6. Surveys and Monitoring

The locations of some of the major river systems within the Northern Territory are shown on Figure 2.

I. *Crocodylus johnstoni*

Annual spotlight surveys in each of the *C. johnstoni* management areas have been carried out in 1985 and 1986, and a detailed analysis of the impact of harvesting is underway with data from 1982 to 1986. Preliminary results (Table 2; CCNT 1986d) indicate no major effects of the harvests could be detected; 6331 eggs and hatchlings were harvested from the areas included in Table 2, yet the sighted population increased from 2859 to 3316 animals.

Table 2. Preliminary data on the impact of harvesting *Crocodylus johnstoni* eggs and hatchlings. Data included are from isolated pools and sections of mainstream in which the entire area was surveyed before and after harvests. First surveys were in 1982 or 1983 and the latest surveys in 1985. Numbers harvested are accumulated totals of eggs and hatchlings.

| Area | Interval | Harvest | | Surveys | |
|------------------|----------|---------|------------|---------|------|
| | | Eggs | Hatchlings | First | Last |
| Finniss/Reynolds | 1983-85 | 1817 | 81 | 196 | 207 |
| Finniss/Reynolds | 1983-85 | 396 | 26 | 108 | 89 |
| Upper Daly | 1983-85 | - | 985 | 503 | 450 |
| Lower Daly | 1983-85 | 434 | 1117 | 664 | 494 |
| Baines | 1983-85 | - | 384 | 272 | 421 |
| Lower Victoria | 1983-85 | - | 128 | 152 | 318 |
| Lower Victoria | 1983-85 | - | 187 | 180 | 233 |
| Upper Victoria | 1982-85 | - | 480 | 318 | 331 |
| Wickham | 1982-85 | - | 71 | 166 | 135 |
| Wickham | 1982-85 | - | 24 | 97 | 100 |
| TOTALS | | 2647 | 3684 | 2859 | 3316 |

Crocodylus johnstoni is a difficult species to survey by spotlight, because many of the areas they occupy recede to small isolated pools in the dry season. Helicopter survey offers a viable alternative to spotlight counting (Bayliss et al. 1986), and in 1985 all areas surveyed for *C. johnstoni* by spotlight were also surveyed from helicopters.

ii. *Crocodylus porosus*

During 1985 and 1986, spotlight surveys have been carried out by the CCNT in the three river systems from which eggs were collected (Adelaide, Finniss and Reynolds) and in a series of rivers from which eggs were not collected. In addition, helicopter surveys were carried out in some rivers. These data are discussed by Webb et al. (this volume), but are also summarized in Table 3 (1984 data are included for comparison). Additional spotlight surveys within the Northern Territory (1985-86) have been carried out by ANPWS and Messel et al. (1986).

Table 3. Densities of *C. porosus* recorded in spotlight counts carried out in major river systems 1985-86 by CCNT, ANPWS¹ and Messel et al. (1986)², with the results of 1984 surveys for comparison. Densities are numbers of *C. porosus* sighted per kilometer subdivided into "all crocodiles" (T) and "non-hatchlings" (NH). "*" indicates helicopter survey corrected to spotlight counts (no hatchlings are accounted for).

| Area | 1984 | | 1985 | | 1986 | |
|----------------------------------|------|------|-------------------|-------------------|------|-------|
| | T | NH | T | NH | T | NH |
| Adelaide | 2.72 | 2.41 | 2.41 | 1.96 | 2.59 | 2.14 |
| Blyth-Cadell R. | 4.00 | 3.53 | 2.48 | 2.03 | 5.65 | 3.25 |
| Daly R. | 1.94 | 1.94 | 2.62 | 2.49 | 3.13 | 2.93 |
| East Alligator R. ¹ | 4.05 | 3.23 | 4.65 | 3.59 | - | - |
| Finniss R. | 3.14 | 3.09 | 3.93 | 3.79 | 2.86 | 2.86 |
| Liverpool-Tomkinson R. | 2.19 | 2.03 | - | - | 2.89 | 1.75 |
| Limmen Bight R. | - | - | 0.24 ² | 0.23 ² | - | 0.29* |
| Mary R. | 1.55 | 1.55 | 1.54 | 1.54 | 2.20 | 2.20* |
| McArthur R. | - | - | 0.21 | 0.20 | - | 0.22 |
| Reynolds R. | 4.38 | 4.18 | 5.04 | 4.93 | 5.21 | 4.99 |
| Roper R. ² | - | - | 1.52 | 1.36 | - | - |
| Towns R. ² | - | - | 0.49 | 0.49 | - | - |
| Wearyan-Foelsche R. | - | - | 0.12 | 0.12 | - | 0.15* |
| Wearyan-Foelsche R. ² | - | - | 0.14 | 0.14 | - | - |

In 1986, helicopter and spotlight counts were carried out in rivers of the southern Gulf of Carpentaria as a check on the previously derived calibration between the two methods (Bayliss et al. 1986). The results (Webb et al. [this volume]) fully supported the use of the Adelaide River calibrations in the Gulf of Carpentaria.

Nest counts appear to be the only usable index of the population size in heavily vegetated freshwater swamps, and correction factors have now been derived for relating nest counts to absolute numbers of *C. porosus* (see Webb et al. [this volume]). These indicate one nest is the equivalent of 17.6 *C. porosus* (15.5 non-hatchlings), or that 5.7% of the population in breeding areas are nesting females. This value is almost identical to that found with *Alligator mississippiensis* in Louisiana (Joanen and McNease 1987).

Rates of *C. porosus* population increase within the Northern Territory have been calculated for all rivers in which survey data span three or more years (Webb et al. [this volume]). The mean rate of increase is +8.3% p.a. for all crocodiles and +9.7% p.a. for non-hatchlings.