

**Broad Scale Influences on Contemporary Abundance of
Saltwater Crocodiles (*Crocodylus porosus*)
in Northern Australia**

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“This thesis was submitted by Yusuke Fukuda as a partial fulfilment of the requirements for the Degree of Bachelor of Science with Honours in the School of Biological, Environmental, and Chemical Science, Faculty of Health, Education, and Science, Charles Darwin University in November 2004.”

“I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published and unpublished work of others has been acknowledged in the text and a list of references given.”

Yusuke Fukuda

22 November 2004

“Mirai ha jibun de tsukuru mono.
Anata ga miru yume no subete koso anata jishin desu.”

Tomoyasu Hotei

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Abstract

Populations of the Saltwater crocodile *Crocodylus porosus* in northern Australia were severely depleted due to uncontrolled commercial hunting from the 1940s to 1970s. Since legal protection in the 1970s, recovery of the species has been carefully monitored across north Australia. Population data accumulated from these monitoring surveys consistently show that the Northern Territory has achieved much greater increases in population number than in Queensland and Western Australia. The difference in population abundance between the Northern Territory and the other States has been linked to a number of different aspects of the environment including natural feature and human impacts. However, the nature of the relationship between population abundance and the quality of the environment remains unclear.

To examine potential species-environment relationships, I proposed that the status of contemporary crocodile populations is most influenced by the environment, rather than the residual effects of past hunting. I first examined this hypothesis by comparing density estimates for contemporary and pre-hunting populations in a range of rivers in the Northern Territory. The comparison showed a reasonable match between the contemporary and pre-hunting populations, suggesting that the populations have recovered to levels broadly comparable with status prior to commercial hunting.

To further test this hypothesis, I then examined trends in population growth of the rivers since their protection by fitting a range of population growth models using information theoretic approach. For the most frequently surveyed major river systems, the information theoretic criteria showed strong support for the logistic model rather than the linear and exponential models. The predicted carrying capacities were close to the observed contemporary densities, which suggests that the recovery of populations is well advanced in most river systems of the Northern Territory and the rate of population increase is now being limited by the quality of the environment rather than the impact from past hunting.

Having found support for this hypothesis, I then developed hypothesis-driven models about relationships between population abundance and the environment based on the species' biology and ecology. The fit of these models was also examined using the

information theoretic procedures. The results showed strong evidence for a model with natural environmental variables namely ‘the mean temperature in the coldest quarter of a year’, ‘the ratio of total area of freshwater wetland dominated by the *Melaleuca* species and seasonal floodplain dominated by the grass and sedge to total area of catchment or subcatchment’, and ‘the ratio of total precipitation in the warmest quarter of a year to total precipitation in the coldest quarter of a year’. The results also showed no strong support for models incorporating human-impact variables, suggesting that contemporary population abundance of the species appears to be primarily influenced by the quality of the natural environment rather than the contemporary impact of human activities. However, further examination of these questions using different datasets at finer spatial scales is desirable.

The natural environmental factors selected as best describing the variation in population abundance of *C. porous* in northern Australia are all likely affected by increase in temperature, precipitation, and sea level due to global warming. Maintaining favourable vegetation communities in freshwater wetlands and seasonal floodplains seems the primary management issue for maintaining the species abundance and its large contribution to the environment and economy of northern Australia.

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CHAPTER 1

Thesis Introduction

1.1. Introduction

Two crocodylian species occur in Australia: the Freshwater crocodile *Crocodylus johnstoni* and saltwater crocodile *Crocodylus porosus*. Both species are distributed in monsoonal tropical regions across northern Australia. Unlike *C. johnstoni*, which is generally restricted to freshwater, *C. porosus* can be found in both fresh and saline water bodies (Webb and Manolis 1988). The habitats they use are consequently diverse, including tidal rivers and wetlands with brackish water, swamps, and floodplain and billabongs with freshwater. Some are found in the ocean along coasts (Webb and Manolis 1993).

Crocodylus porosus was once threatened across its northern Australia range by intensive hunting for the skin trade from the 1940s to early 1970s (Webb and Manolis 1993b, Cooper-Preston and Jenkins 1993). The remarkable reduction in population due to the commercial hunting led legal protection of the species in the early 1970s. Over more than 30 years of protection, population change has been closely monitored in the States and the Northern Territory (Webb *et al.* 1998, Western Australian Department of Conservation and Land Management (CALM) 2003, Parks and Wildlife Management Service of the Northern Territory (PWSNT) 2004, Read *et al.* 2004). Those monitoring surveys have shown a positive response of the species to protection, which allowed re-establishment of a crocodile industry based on sustainable use of the species as part of their conservation (Cooper-Preston and Jenkins 1993, Webb and Manolis 1993a, PWSNT 2004). Harvesting is closely regulated by relevant government agencies.

While population abundance is increasing across northern Australia, data accumulated from the monitoring surveys show consistent differences in population density between the States and Territory. The Northern Territory has much higher densities than in Queensland and Western Australia (Webb and Manolis 1993a). Recent studies imply that some of the Northern Territory population is even approaching full recovery (Webb *et al.* 1998, PWSNT 2004), while the populations in the Queensland

and Western Australia are smaller (Cooper-Preston and Jenkins 1993) and their recovery is marginal or limited (Mawson 2004, Read *et al.* 2004).

The differences in population abundance between the States and the Northern Territory have been linked to certain aspects of the environment, including natural features and human impacts. More specifically, it is speculated that some human activities such as urban development and agriculture are limiting the recovery on the east coast of Queensland (Taplin 1987, Taplin 1990, Cooper-Preston and Jenkins 1993, Webb and Manolis 1993a, Kofron and Smith 2001). In contrast, variation and gradation in natural environmental variables such as climate and topography have been suggested as influences on crocodile abundance, especially in Western Australia (Preston and Jenkins 1993, Webb and Manolis 1993a, CALM 2003). The relationship between population abundance and environment, however, remains unclear. There is no detailed information on the undoubtedly complex species-environment relationship available (Taplin 1987, Taplin 1990, Webb 1991). Quantitative analysis of broad-scale variations in population abundance is necessary to examine what environmental factors influence the population abundance and how strongly these factors influence abundance. Interpretation of the relationship in biological and ecological terms should provide new information and insights required for the future management of crocodiles in Australia. In particular, better understanding of natural influences on crocodile distribution and abundance will help identify where populations are anomalously low, and hence where human impacts may be limiting populations.

1.2. Study aim and objectives

The aim of this biogeographic study is to examine the extent of population recovery of *C. porosus* and determine what environmental variables most likely influence patterns in population abundance in northern Australia.

Within this overall aim, the objectives are to:

- compare the contemporary population abundance to levels before commercial hunting;
- examine changes in population abundance over the period of recovery;

- build hypothesis-based statistical models of the relationship between abundance and environmental features;
- characterize catchments in northern Australia in terms of relevant environmental features identified during the literature review and chosen from the available datasets characterizing the Australian tropics;
- construct and rank the plausibility of alternative abundance-environment models; and
- discuss implications of the results in terms of crocodile management across northern Australia.

1.3. Background

Saltwater crocodile *Crocodylus porosus*

Both the Australian crocodile species, *C. johnstoni* and *C. porosus*, are ‘true’ crocodiles (family Crocodylidae), as distinct from the other two families of the Alligatoridae (alligators and caimans) and Gavialidae (gahrials) (Webb and Manolis 1993a), which are the only living members of the suborder Eusuchia that contains both extinct and extant species. All other suborders are restricted to fossil forms (Cogger 1993). Some males of *C. porosus* grow to more than 5 m in total length and consequently it is the biggest species among the extant crocodilians (Webb and Manolis 1993a).

While the Australian freshwater crocodile is endemic to Australia, the saltwater crocodile is widely distributed. Its range includes Sri Lanka, eastern India, the Andaman and Nicobar Islands, and Bangladesh in the west, through coastal southeast Asia to the Philippines, Western Carolines in the north, and south through Indonesia to Papua New Guinea and northern Australia, east to the Solomon Islands and Vanuatu (Groombridge 1993). Despite its wide distribution, the species is considered threatened or endangered in many countries due to extensive hunting for skins and habitat destruction (Groombridge 1987).

In Australia, the species is distributed along northern coastal regions from Broome in Western Australia in the west through the Northern Territory to Rockhampton in Queensland in the east (Webb and Manolis 1993) (Figure 1.1). These regions represent the tropics of Australia and are typically dominated by a monsoonal climate. Within these regions, *C. porosus* inhabits coastal water bodies within approximately 100 km of the sea, although some are found more than 200 km upstream in major rivers (Webb and Manolis 1988). The species is most abundant in tidal rivers, creeks and wetlands containing brackish water, and floodplains, swamps and billabongs with freshwater. They are also less commonly found in the ocean along the coastline, perhaps travelling between river systems (Webb and Manolis 1993, PWSNT 2004).

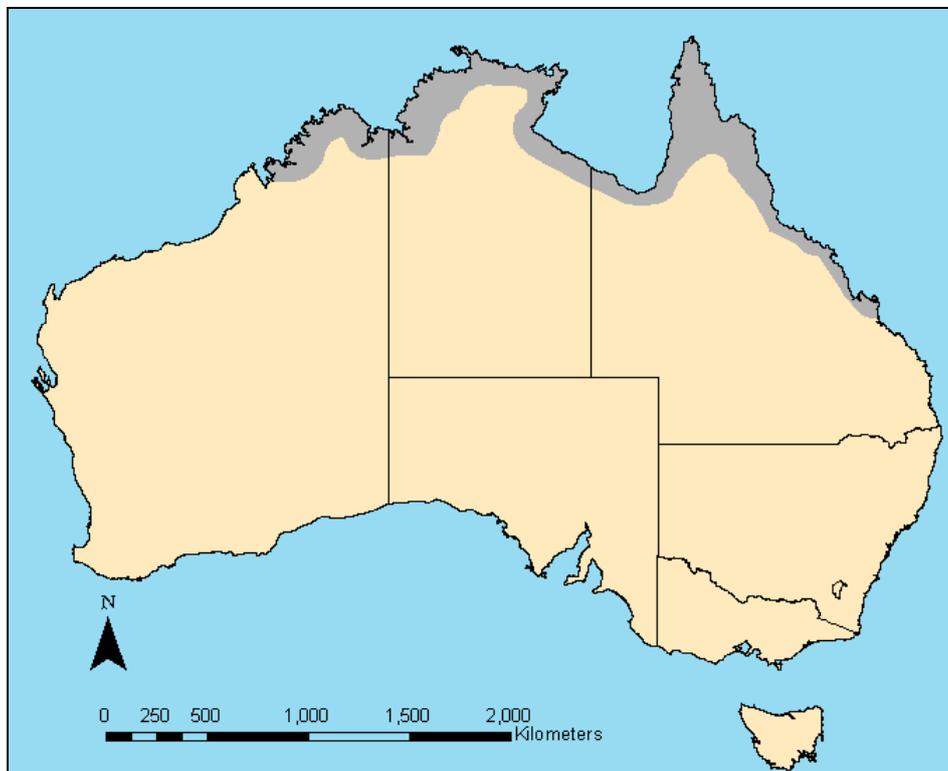


Figure 1.1. Distribution of *C. porosus* in Australia (shaded in grey) (crocodile distribution data from PWSNT 2004).

Management history

Saltwater crocodiles have been hunted by human beings for a long period of time, probably since the first contact with humans. Crocodile meat and eggs are thought to have been used as a food source by Aboriginal people for up to 40 000 years, just as they are today in northern Australia (Cooper-Preston and Jenkins 1993, PWSNT

2004). This form of harvesting seems to have had no major impact on the population size of the species (Altman 1987, Webb and Manolis 1993a). However, intensive commercial hunting for the skin trade that began in 1945 resulted in a remarkable depletion in crocodile numbers across northern Australia. The uncontrolled exploitation was most directed at *C. porosus* and continued until the early 1970s. Although there are no definitive data on the population size immediately after the over-hunting, it is estimated that the total harvest during the period was 330 000 animals of which 140 000 were from the Northern Territory and 190 000 were from Queensland and Western Australia (Webb *et al.* 1984, Webb *et al.* 1987, Webb and Manolis 1993a).

Following the significant decline of crocodiles, hunting was prohibited by the State and Territory legislators and the species was legally protected. Protection was done first in Western Australia in 1970, followed by the Northern Territory in 1971, and in Queensland in 1974. The Federal Government also banned the export of crocodiles and their products in 1972.

In 1975, *C. porosus* was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (PWSNT 2004). CITES is an international agreement between governments to regulate trade in endangered wildlife species. Appendix II is defined to include species not necessarily threatened with extinction, but which may be if trade is not strictly controlled (Cooper-Preston and Jenkins 1993, CITES 2004). In 1979, all Australian populations of *C. porosus* were transferred to Appendix I that includes species considered to be threatened with imminent extinction (Jenkins 1987, PWSNT 2004). As they were shown to have started responding positively to protection (Webb *et al.* 1984), the Australian populations were transferred again, from Appendix I to Appendix II, in 1985 (PWSNT 2004). This transfer allowed the re-establishment of crocodile industries based on controlled harvesting and farming in Australia.

Current crocodile management

The State and Territory Governments have principal responsibility for conservation and management of crocodiles (Cooper-Preston and Jenkins 1993): PWSNT in the

Northern Territory, Queensland Parks and Wildlife Service (QPWS) in Queensland and CALM in Western Australia. These organizations control crocodile management by monitoring crocodile populations, regulating commercial harvesting and farming, and securing public safety against crocodile-human conflicts.

The crocodile management programs essentially focus on the conservation of the species as a sustainable resource (Webb and Manolis 1993a, CALM 2003, PWSNT 2004). The commercial value of crocodiles provides incentives for land managers to conserve crocodiles and their habitats as landowners are paid royalties by harvesters for each egg or animal collected from their property.

A regulated commercial industry for skin, meat and other crocodile products, based on captive breeding and ranching of wild-harvested eggs at licensed farms commenced operating in 1980 in the Northern Territory, 1983 in Western Australia, and 1984 in Queensland (Cooper-Preston and Jenkins 1993, CALM 2003, PWSNT 2004). There are currently six farms operating in each of the Northern Territory and Queensland jurisdictions, and two in Western Australia (PWSNT 2004, Mawson 2004, Read *et al.* 2004).

Wild egg harvesting is a major form of harvesting to supply stocks in captivity. To a lesser extent, juveniles and adults are also harvested, including 'problem' crocodiles removed from the wild for public safety. Problem crocodiles are animals that potentially impose risks to human and livestock, such as in popular public areas for recreation. Animals removed may be kept in captivity as breeding stock or used for commercial production. The Northern Territory commenced adult harvesting for immediate commercial production in 1997 (PWSNT 2004). The maximum number of eggs and animals that may be taken from the wild is strictly set as a sustainable harvesting quota in each Territory and the States (CALM 2003, PWSNT 2004, Read *et al.* 2004). The quota is determined based on the results of annual population monitoring programs so that the harvesting will not be detrimental to wild populations.

Current population status

Since their legal protection, the recovery of crocodile populations has been carefully monitored and summarized in the States and Territory (e.g. Bayliss *et al.* 1986, Webb and Manolis 1992, Webb *et al.* 1998 for the Northern Territory, Taplin 1987, Miller 1994, Kofron 1999 for Queensland, Burbidge 1987, Wildlife Management International (WMI) 1992, CALM 2003 for Western Australia). Messel *et al.* (1979) initiated systematic population surveys in northern Australia and presented the results as a series of Monographs (1979-1987). The Territory and State Government agencies have undertaken monitoring surveys with inputs from private organizations such as WMI since the Messel surveys ceased.

As populations recovered over time, these studies found that the Northern Territory contains a much higher population than the other States. Since protection in 1971, the *C. porosus* population has consistently increased in the Northern Territory from an estimate of around 3000 non-hatchling individuals to between 30 000 and 40 000 in 1984 and between 70 000 and 75 000 in 1994 (Webb *et al.* 1998, PWSNT 2004). Recent surveys conducted by PWSNT have been interpreted as suggesting that populations in major rivers, such as the Adelaide River, are approaching an asymptote, and therefore probably reaching the maximum carrying capacity. The high rate of recovery is thought to have been due to the continued abundance and high quality of habitats available in the Northern Territory (Webb and Manolis 1993a). On the contrary, populations in Queensland and Western Australia have shown limited recovery with low to moderate increase over time (Kofron and Smith 2001, CALM 2003, Read *et al.* 2004). Both population abundances and rate of increase are much lower than those of the Northern Territory.

The difference in the size of contemporary populations may be reflected in current territory and state legislation. Saltwater crocodiles are currently listed as “a species of least concern” under the *Territory Parks and Wildlife Conservation Act 2000* in the Northern Territory (PWSNT 2004), “vulnerable” under state conservation legislation in Queensland (CALM 2003, Read *et al.* 2004), and “otherwise specially protected” under the *Western Australian Wildlife Conservation Act 1950* in Western Australia

(where “otherwise specially protected” refer to fauna that require special protection for reasons other than that they are rare or likely to go extinct) (CALM 2003).

Species-environment relationship

While the extensive monitoring research of crocodiles shows the highly variable levels of population abundance and rate of increase, the relationship between population abundance and local environments has been speculated upon in an informal fashion.

It is often postulated that certain human activities are keeping crocodile numbers low, particularly in the eastern coast of Queensland (Taplin 1987, Taplin 1990, Cooper-Preston and Jenkins 1993, Kofron and Smith 2001). While Northern Territory habitats remain relatively intact, much of the habitat in Queensland has been subject to extensive modification for agriculture, tourism and residential development (Cooper-Preston and Jenkins 1993). Taplin (1987) also speculated about natural factors such as climatic variables, and noted that ‘virtually nothing is known about physiological and ecological adaptations of *C. porosus* to the climatic gradients in Australia’. He suggested minimum temperatures in the winter (dry season) as a limiting factor of their distribution in south Queensland. Webb (1991) also summarized the influence of season on the behavioural ecology of Australian crocodiles, also noting the limited information available on the relationship.

In Western Australia, it is speculated that the available habitats have only ever supported smaller crocodile populations than the Northern Territory (Webb and Manolis 1993a, CALM 2003). Factors such as lower rainfall, limited riparian vegetation and higher cattle grazing pressure are suggested to have had an impact on the size of population in Western Australia (Mawson 2004).

However, the relationship between these environmental variables and crocodile population has never been quantified. It therefore remains unclear whether the differences in crocodile abundance between the Territory and States derive from natural or human-induced factors.

Physiological studies have examined the influence of certain environmental conditions on individual animals, such as ambient temperature (Lang 1987, Gordon and Seebacher 2000) and water salinity (Grigg *et al.* 1980, Grigg *et al.* 1986).

Since crocodiles are ectotherms, their body temperature is controlled by their behaviour in relation to the thermal heterogeneity of the habitat, modified by physiological mechanisms. In *C. porosus* in northern Australia, body temperatures are around the ambient water temperature, commonly 25 to 28 °C, and their upper lethal temperature seems to be about 35 °C (Grigg and Guns 1993).

For water salinity, Grigg *et al.* (1986) observed that *C. porosus* living in natural hyperosmotic environments has lower field efflux of salt than the maximum measured in the laboratory. Hatchlings of *C. porosus* are also known to survive and grow in hypersaline habitats with salinity nearly twice that of seawater (Grigg and Guns 1993). However, it is unknown whether they could survive without drinking fresh water. Much of the physiological and anatomical knowledge available is limited to the laboratory and their importance and relevance to wild animals remains to be determined (Grigg and Gans 1993, Grigg and Seebacher 2000).

These studies are too limited to provide more than very broad indicators of likely environmental influences on *C. porosus* distribution and abundance. The relationship between the environment and *C. porosus* therefore remain unclear. The species-environment relationship is apparently complex with a number of environmental factors simultaneously affecting crocodile populations and their effects being modifiable by behaviour (Lang 1987, Taplin 1987, Taplin 1990, Webb 1991, Grigg and Seebacher 2000). It remains to be examined what aspects of the environment most strongly influence population abundance and how strong these relationships are. To answer this question, it is necessary to develop population models of the species in relation to the environment. Feasible inference based on the models incorporating features that may influence quality of habitat can provide new information on the abundance-environment relationship at a national scale.

Geographic Information System and ecological modelling

Examining the relationship between wildlife species and environment requires the development of realistic models representing species distributions and aspects of the environment that influence the suitability of habitat (Haines-Young *et al.* 1993, Koeln *et al.* 1996, Johnston 1998). This essentially involves analysis and mapping of the environmental resources on which the animals depend (Leeuw *et al.* 2002). A Geographic Information System (GIS) has been playing an important role in this aspect of ecological modelling, providing efficiency and effectiveness in mapping and analysis of wildlife distribution and abundance in relation to the physical and human environment (Koeln *et al.* 1996, Hollander 1998, Leeuw *et al.* 2002). GIS is defined as ‘an organized collection of computer hardware, software, geographic data, and personnel designed to efficiently capture, store, update, manipulate, analyze, and display all forms of geographically referenced information’ (ESRI 2004).

GIS has shown its value particularly in studies to model distribution and abundance of threatened wildlife populations in relation to their environments. Jaberg and Guisan (2001) examined the relationships of endangered bat species (*Vespertilio murinus*, *Eptesicus nilssoni*, *E. nathusii* and *Myotis myotis*) with the landscape in western Switzerland. They constructed quantitative models based on landscape structure to predict spatial patterns in species composition and individual species’ distribution using a GIS. The results showed that the community composition and species distribution are related to specific landscape structure through species-specific relationships to resources. Li *et al.* (2002) developed a habitat suitability model to evaluate habitat quality for seriously threatened crested ibis (*Nipponia nippon*) in China. Their resulted habitat suitability map integrated in a GIS highlighted potential influences of certain environment variables on the species. A similar habitat suitability model was built for endangered brown bears (*Ursus arctos*) in northern Spain (Naves *et al.* 2003). A GIS was effectively used to quantify certain environmental variables specific to the species for predicting their mortality and reproduction.

GIS has also been used in habitat suitability analyses of *C. porosus* in the Northern Territory. Harvey and Hill (2003) integrated remotely sensed geographic data in a GIS

to model habitat suitability for nesting by the species in the Adelaide River region. They effectively integrated environmental data as criteria for nesting such as vegetation type and distance to water and showed some potential to identify existing preferred nesting areas in the region. In a similar fashion, Fukuda *et al.* (2004) predicted the suitability of catchments as *C. porosus* habitats in the north-west region of the Northern Territory, using a GIS-based model. The predictive model was composed from a range of topographic features that were considered as surrogates for suitable habitat based on the literature and expert opinions about the species. A simple validation of the model showed a relatively high correspondence between the prediction and actual population data. However, although these studies provide important pointers to the relationship between the species and environment, neither of the predictive models quantified the potential influences of the identified environmental variables on the species' abundance.

1.4. Research overview

The study consists of three main components (Figure 1.2). The first is a historical population analysis that compares contemporary populations of *C. porosus* to populations estimated to be in existence prior to uncontrolled commercial hunting. Results of this comparison should provide some insights for the extent of recovery in the contemporary populations. This study is obviously limited to those areas in which pre-hunting data exist.

The second analysis then focuses on trends in population recovery for selected rivers. Population abundance indices over 24 years from the extensive monitoring surveys are examined by fitting a range of models (linear, exponential and logistic) for population growth. The pattern of population recovery is inferred for each river based on the fit of each model. The model that best approximates each crocodile population dataset is determined, using the Information-theoretic paradigm suggested by Burham and Anderson (1998; 2001; 2002). This analysis essentially examines whether the population is still recovering (linear or exponential growth) or reaching the maximum carrying capacity (asymptotic growth).

The third component of this study models the abundance-environment relationship for contemporary *C. porosus* populations across northern Australia. The population abundance indices are derived from monitoring surveys conducted by relevant agencies and the environmental variables are calculated using a GIS. The ecological modelling is conducted using information-theoretic procedures as above. This involves developing a set of candidate models based on hypotheses reflecting biological and ecological knowledge of the phenomenon of interest. In this case, distribution and abundance of *C. porosus*. The set of candidate models will include both natural features and human impacts on crocodiles or their habitats and are derived statistically using Generalized Linear Modelling (GLM). The candidate models are ranked and the relative importance of each variable is also determined.

The abundance-environment relationship derived from the models is then interpreted in terms of the biology and ecology of the species. Implications for crocodile management in Australia and limitations of the results are also discussed.

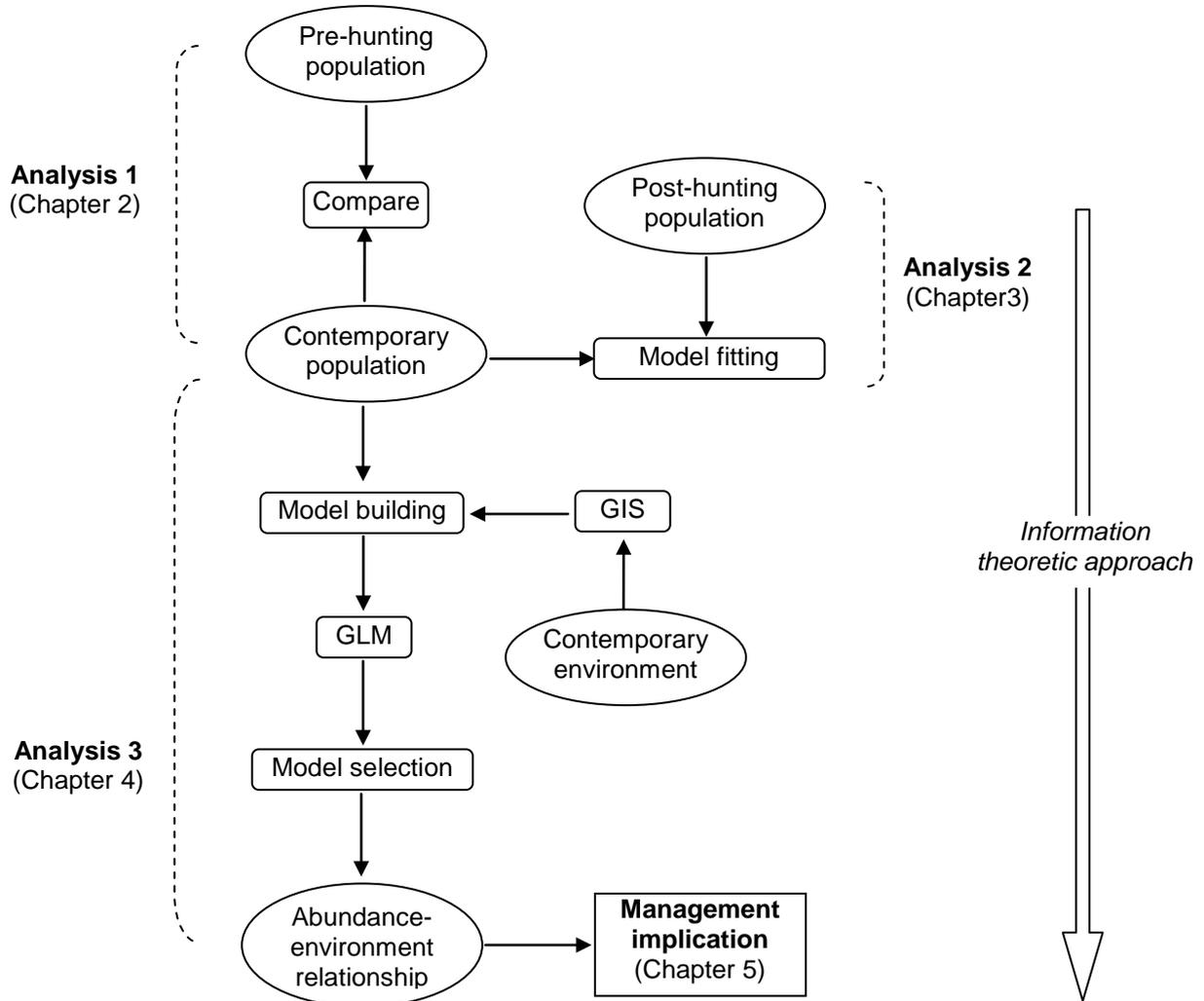


Figure 1.2. Research overview. The study consists of three analyses: Analysis 1 compares population abundance of *C. porosus* between the contemporary and pre-hunting periods (pre-hunting – contemporary), Analysis 2 examines patterns of population recovery (post-hunting – contemporary), and Analysis 3 is modelling of the contemporary population abundance-environment relationship.

CHAPTER 2

Comparison of Pre-Hunting and Contemporary Abundance

2.1. Introduction

Commercial hunting for the skins led to substantial declines in the abundance of *C. porosus* in northern Australia (Webb and Manolis 1993b, Webb *et al.* 1998, PWSNT 2004). Although the size of 'pristine', pre-hunting population remains uncertain, the population at the time of protection was undoubtedly very small compared to the capacity of the environment to support crocodiles. The recovery of *C. porosus* populations from commercial hunting in the period following the Second World War has been extensively monitored since their legal protection, particularly in the Northern Territory (PWSNT 2004).

Messel *et al.* (1979) and his colleagues conducted the first systematic population surveys of the species in major rivers across the Northern Territory, and parts of Queensland and Western Australia. They established the methodology for spotlight surveys that counts eye-shines of crocodiles in a spotlight so that the counts can be standardized and presented as a population abundance index (sightings per km of river). Results of their survey were summarized as Monographs (1979-1987) and provide important information on crocodile abundance in the early periods after commercial hunting was made illegal.

Since the Monographs era, relevant State and Territory organizations such as PWSNT, QPWS and CALM have undertaken additional crocodile surveys. Although some rivers were replaced with helicopter counting surveys in the Northern Territory and Western Australia (Bayliss 1987, WMI 1992, Webb *et al.* 1998, CALM 2003), the spotlight surveys are still conducted annually in many of the major rivers, with minor change in methodology. A number of monitoring studies consistently showed significant increases in crocodile numbers, particularly in the Northern Territory (e.g. Bayliss *et al.* 1986, Webb *et al.* 1990, Webb and Manolis 1992, Webb *et al.* 1998) (Figure 2.1).

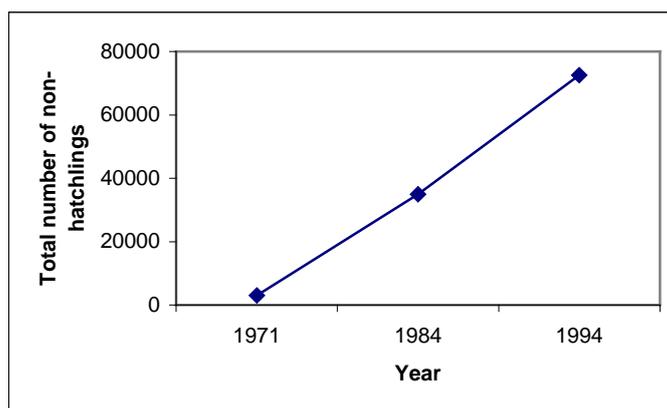


Figure 2.1. Total number of *C. porosus* non-hatchlings (> 2 feet or 60.96 cm) in the Northern Territory, estimated from spotlight and helicopter survey counts (Webb *et al.* 1998, PWSNT 2004). In both helicopter and spotlight surveys, the size of individual is usually estimated in 'feet' rather than 'meters' because 'feet' adequately approximates the range of crocodile sizes (<0.6-5m or <2-17 feet) in a manageable number of increments, while the scale of 'meter' is too broad and 'centimeter' is too fine (Webb *et al.* 1998).

However, recent monitoring studies have shown that the relative rate of increase has slowed in some major rivers of the Northern Territory, suggesting that populations may have recovered to levels approaching carrying capacity (Webb *et al.* 1998, Webb *et al.* 2000, PWSNT 2004). The implication of this argument is that population densities have recovered to levels existing before intensive hunting.

If populations are indeed approaching carrying capacity then, by definition, the density of animals will be most strongly influenced by the quality of environment, and the animals' interactions with the environment, rather than past harvests.

In this analysis, I examine the notion that the recovery of population levels is well advanced and perhaps complete, under prevailing environmental conditions. In particular, I compare contemporary measures of population density with estimates of population density made from the accounts of hunters and others familiar with crocodile populations prior to the commencement of intensive hunting (see Webb *et al.* 1984).

2.2. Methods

Two datasets were required for this analysis: 1) estimates of population density before intensive hunting and 2) contemporary data consisting of the most recent measures of

population densities of rivers in the Northern Territory. The pre-hunting data were derived from a technical report presented by Webb *et al.* (1984). The contemporary data were collected from different available sources. Descriptions and sources of these datasets are provided below.

Pre-hunting data

Intense commercial hunting in the Northern Territory began in 1945. The estimates of pre-hunting population abundance were based on interviews by Webb *et al.* in 1984 with early hunters who operated during 1945-48 in rivers, creeks and sections of coast of the Northern Territory. The hunters interviewed considered themselves the first professional hunters in those areas. Although Aboriginal people hunted crocodiles as a food resource, contemporary studies (Altman 1987, Webb and Manolis 1993a) indicate that the number of crocodiles taken by Aboriginal people in customary harvests is relatively small and unlikely to have suppressed populations substantially.

Webb *et al.* (1984) presented a crocodile abundance index based on the observations and perceptions of these hunters as “first hand accounts of what was probably the situation which existed at the time of European contact”. The hunters’ estimates of abundance referred to all size classes of crocodiles from hatchlings (< 2 feet) to large individuals. The estimation is specific to certain sections of rivers where crocodiles were most abundant and thus the commercial hunters most often visited (Table 2.1), since crocodiles never appear to have been distributed evenly along rivers (Webb *et al.* 1984, Webb *et al.* 1987). The hunters’ estimates were converted to three classes of spotlight count relative density by Webb *et al.* (1984) to make the estimation comparable with the spotlight-count density index. It was based on how many crocodiles hunters usually saw per km in those sections of river (C. Manolis, pers. comm. WMI 2004). The three classes are High (6-12 sightings/km), Medium (1-5 sightings/km) and Low density (<1 sightings/km).

The analysis was possible only in the Northern Territory due to the lack of comparable data on crocodile populations before commercial hunting in the other states (Queensland and Western Australia).

Contemporary data

Over the 30 years since protection, PWSNT, WMI, and Parks Australia North (PAN) have monitored saltwater crocodile populations in a number of river systems of the Northern Territory. The contemporary data for population abundance in this study were provided by these organizations. Depending on the river, data were collected in either helicopter or spotlight surveys. Rivers with spotlight count data available were chosen from those that appear in the pre-hunting datasets, since the pre-hunting data are formatted in spotlight count relative densities. The most recent year available in spotlight count ranged from 1992 to 2003 among the rivers. The densities included all size classes (i.e. hatchlings) to allow relevant comparison with the pre-hunting data. Those densities were calculated from raw counts without correcting for visibility bias. In most rivers, it was possible to match surveys for the same sections of the river as used for the pre-hunting data because of their distinct locations (Table 2.1).

Table 2.1. Particular sections of the rivers used for the contemporary density. Local names are those of crocodile data in the Northern Territory used by researchers. Start and end points are starting and ending points of surveys indicated as longitude and latitude in decimal degrees reprojected in the Geocentric Datum of Australia 94 (GDA94). Note that the Glyde River (billabong) refers to only one location (Old Arafura Billabong) while the pre-hunting data refers to two locations (Old Arafura Billabong + Floodplain Billabong) due to limited availability of data for contemporary populations. Similarly, the contemporary Finnis River data refer to one location (Patj Patj) although the pre-hunting includes another location (Bullcoin).

River	Local Name	Start Point	End Point
Mary River	Sampan creek to Shady camp	131.7787 -12.2648	131.7070 -12.2689
Adelaide	Mainstream (0 - 117 km)	131.2346 -13.1221	131.2224 -13.1238
Wildman	Mainstream	132.0554 -12.2878	132.1300 -12.3110
Daly	Mainstream	130.7073 -13.7690	130.3088 -13.7622
Finnis	Patj Patj	130.5051 -13.0246	130.5276 -13.0246
Reynolds	Welltree lagoon	130.5047 -13.1915	130.5524 -13.1893
	McEddys lagoon	130.5385 -13.1578	130.5547 -13.1532
East Alligator	Mainstream	132.6941 -12.1151	132.9474 -12.1219
Moyle	Mainstream	129.7448 -13.9784	129.7719 -13.9743
Glyde (billabong)	Old Arafura billabong	134.9556 -12.4863	134.9593 -12.4906
Roper	Mainstream	133.4624 -14.7305	133.5757 -14.7498
West Alligator	Mainstream	132.2971 -12.2187	132.2719 -12.2300
South Alligator	Mainstream	132.3920 -12.4518	132.5218 -12.4529
Blyth	Mainstream	134.5931 -12.0116	134.6768 -12.0070
Cadell	Mainstream	134.5845 -12.1669	134.5147 -12.1759
Liverpool	Mainstream	134.2133 -12.0288	134.1026 -12.0205
Tomkinson	Mainstream	134.1961 -12.1324	134.2783 -12.1421
Glyde (mainstream)	Mainstream	135.0420 -12.2705	134.9967 -12.2741
Victoria	Mainstream (87-145 km)	130.1467 -15.4205	130.4865 -15.4323
Limmen Bight	Mainstream	135.7057 -15.0979	135.4107 -15.4655

2.3 Results

The contemporary density estimates varied substantially among the rivers (Figure 2.2). The densities ranged from 0.31 sightings/km of the Limmen Bight River to 27.60 sightings/km in the Glyde River (billabong).

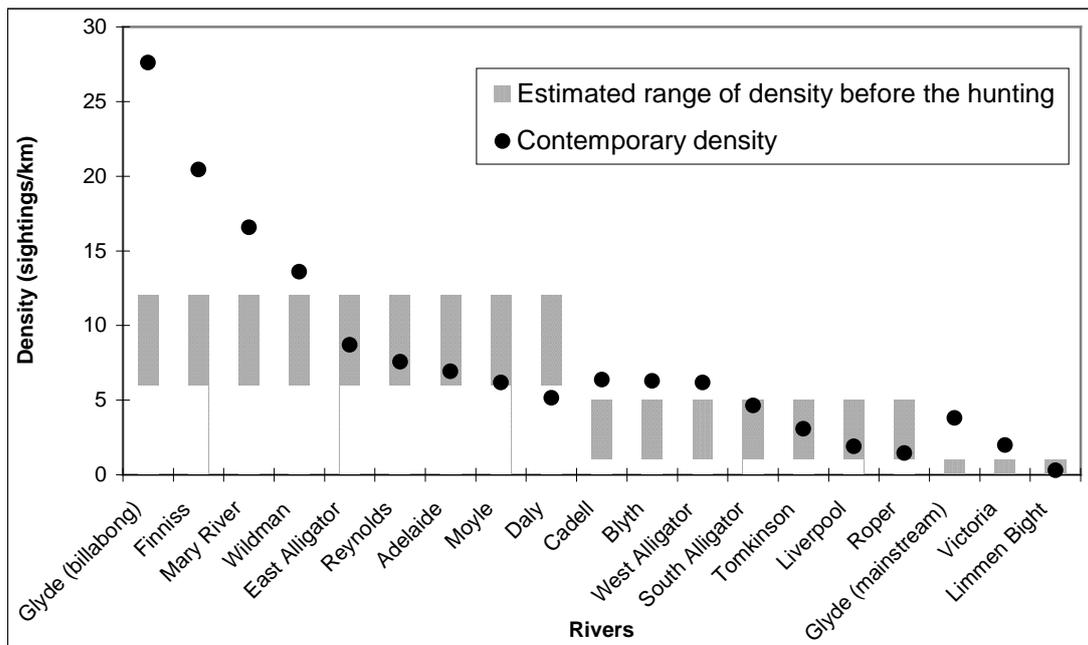


Figure 2.2. Comparison of contemporary estimates of *C. porosus* densities in rivers of the Northern Territory to pre-hunting density classes assigned by professional crocodile hunters active at the commencement of hunting. Note that only one location could be used for the contemporary densities of the Glyde River (billabong) and Finniss River while the pre-hunting estimate for each of these rivers refers to two locations.

In comparison to the pre-hunting period, some contemporary densities were much higher than the upper bound of the high density class identified by the hunters. The Glyde River (billabong) and Finniss River had exceptionally high contemporary densities in the class. Only the Daly River had an observed density below the lower bound of the pre-hunting high density class in nine rivers assigned to the high density class. In the pre-hunting medium class, four rivers of seven fell within the bounds of the class. The other three had slightly higher contemporary densities than the upper bound of the pre-hunting class. Similarly, in the low class, all the contemporary densities were above or within the bound of the pre-hunting class.

In summary, all the rivers except for the Daly River had contemporary densities higher than the lower bounds of the pre-hunting classes, and in many cases very much higher.

2.4 Discussion

The Northern Territory rivers show a wide range of contemporary densities. This level of variation is not unexpected, given the wide range of flow regimes and landscape settings in which those rivers are embedded. Environmental variation that may be associated with variation in crocodile densities is explored in detail in the Chapter 4.

These various contemporary density estimates match reasonably well with the pre-hunting density estimates, with about half falling within the pre-hunting density classes and many showing apparently higher contemporary densities than the upper bound. Only the Daly River had a contemporary density lower than the lower bounds of the pre-hunting classes.

It is important to remember that the pre-hunting data are only estimations based on the collective observations and perceptions of the hunters who operated in the regions. It was not derived from actual spotlight-counting surveys.

In addition, crocodiles are not distributed evenly along a river (Webb *et al.* 1984, Webb *et al.* 1998). Their distribution is highly heterogeneous, concentrating in particular sections of a river while leaving other sections almost vacant. It is possible that there was some mismatching between the particular areas to which the hunters specifically referred and the locations where the contemporary surveys were conducted, such as in the Glyde River (billabong) and Finniss River (Table 2.1).

It is also important to note that year-by-year variation in the environmental conditions such as weather, temperature and tide affect sightability of crocodiles (Bayliss 1987, Webb and Smith 1987, Webb 1991, PWSNT 2004). These environment conditions also influence the abundance of smaller animals, especially hatchlings, by changing breeding success in the year of observation (Webb *et al.* 1998, Webb *et al.* 2000).

Despite these limitations, the comparison suggests that populations across the Northern Territory have recovered to levels at least broadly comparable with those existing prior to the period of intensive hunting (Figure 2.2).

This comparison supports the argument that in recent years populations are approaching or have reached levels near those seen in the absence of significant harvest. It is likely that until commercial hunting began, populations were relatively stable around carrying capacity, with no severe human-induced negative impacts, given that traditional harvesting - as a food source - by Aboriginal people seems to have had a limited impact on population size of the species in northern Australia. Consequently, I conclude that the variation in contemporary *C. porosus* populations across the Northern Territory is strongly determined by the quality of habitat and subsequent resource availability, rather than a legacy of historical hunting activity.

In the next chapter, I provide an additional analysis to further examine this conclusion by looking at historical population abundance of the individual rivers since their protection. Specifically, I examine trends in population growth over the period of recorded data. I seek to determine whether those trends are consistent with patterns of growth expected in the absence of acute human impacts on either crocodile environments or crocodile population density.

CHAPTER 3

Population Growth Pattern after the Hunting in the Northern Territory

3.1. Introduction

In the last chapter, the comparison between the contemporary and pre-hunting crocodile populations suggested that the contemporary populations across the Northern Territory have recovered to be comparable with those before the period of intensive hunting. Assuming that the pre-hunting populations varied around carrying capacity in the absence of serious human pressure, I hypothesised that populations are likely approaching carrying capacity in the contemporary environment. It follows that current populations are now most influenced by the quality of environment rather than the lingering effects of the previous hunting.

However, some ambiguity remains given the origin of estimates of pre-hunting densities, which are based on recollections of sightings rather than formal surveys. In addition, the conclusion was derived from one contemporary observation (the most recent crocodile abundance estimate). Confidence in this conclusion would be increased by independent lines of evidence. I seek this in evidence for stabilisation (plateauing) of counts of crocodiles over the years of population recovery. An approach that takes advantage of a sequence of counts made under a range of environmental conditions will reduce the potential for bias.

In this analysis, I examine sequences of crocodile density estimates made over the years following intensive commercial hunting in individual rivers. Unlike the last analysis where particular sections of the rivers were extracted for density measurements, this analysis incorporates density data for the total length of mainstream and side creeks so that it will reflect population abundance in a whole river system.

Moreover, I examine trends in population abundance of these rivers by fitting a range of population growth models, including asymptotic and non-asymptotic, to the population data. The fit of the models is examined using the information-theoretic procedures developed by Akaike (1973; 1974) cited in Burnham and Anderson (1998;

2001; 2002). The information-theoretic paradigm is a package or integration of a scientific philosophy, analysis strategy, and inferential methodology (Burnham and Anderson 2002). This provides an effective, consistent and practical approach for model selection (Burnham and Anderson 1998). The extent of recovery of populations in these river systems is inferred based on the model that is selected by the information-theoretic approach as best approximating the crocodile population data.

3.2. Methods

The information-theoretic approach essentially provides a simple and practical means for inferential model selection by assessing ‘strength of evidence’ for each model (Burnham and Anderson 1998; 2001; 2002). Burnham and Anderson (2001) emphasize the importance of the philosophical aspects of the information-theoretic paradigm that largely relies on the quality of the science hypotheses to be examined. Each hypothesis in a set should be considered relevant and supported to some extent by the underlying science of interest (Burnham and Anderson 2002). This is an actual distinguishing feature of the information-theoretic approach. Rather than having a null and a single alternative hypothesis, it takes multiple alternative working hypotheses to make formal inference about the science question addressed (Anderson and Burnham 2002). This requires much ‘*a priori*’ consideration to select candidate models even before manipulating data (Burnham and Anderson 1998; 2001).

To examine the trends in population abundance of *C. porosus* in the Northern Territory rivers, three different models were first selected based on available information on crocodile populations and these models. Logic for the selection and descriptions of each model is provided below.

Candidate models

As the simplest model for population growth, a linear regression model was first considered. It essentially assumes that population grow at a constant rate of increase over time. While this is rarely the case in natural populations, the model may adequately describe some population change over a short period (Caughley and Sinclair 1994, Townsend *et al.* 2000, Stiling 2002). Moreover, it may provide some

measure of the rate of short-term increase that a population can afford when the population is freed from constraints usually imposed by limited resources or other unfavourable conditions (Caughley and Sinclair 1994). Given that *C. porosus* populations in the Northern Territory were seriously depressed due to commercial hunting and they have been released from the hunting pressure since 1971, this model may be able to approximate their constant recovery. As the simplest model available for an increasing population, therefore, the linear model was selected as the first hypothesis to be examined in the set. The following equation was specified for the model;

$$y = ax + b$$

Where

y = crocodile density,

x = year since protection (1971),

a = population growth rate, and

b = initial population density in 1971.

After considering the linear regression model, I introduced another model with more realistic growth pattern. Under favourable conditions, a new, expanding population initially shows exponential growth with a constant relative rate of increase but with an increasing absolute rate of increase rather than a constant rate of increase (Townsend *et al.* 2000, Stiling 2002). The exponential growth may occur when species with high fecundity recover from over-exploitation in the past. Stiling (2002) provides useful examples for this type of growth. The northern elephant seal *Mirounga angustirostris* was severely depleted due to intensive hunting for the blubber and fur in the late 19th century. After protection of the species, a population on Año Nuevo Island off the coast of Santa Cruz, California started recovering in 1961, recolonizing their old habitats, and increased exponentially until the 1980s. Whooping crane *Grus americana* showed similar growth (Stiling 2002). The species was nearly extinct due to hunting in the 1940s and populations on the Texas coast recovered exponentially after protection. These examples seem to have important implications for the recovery of *C. porosus* in the Northern Territory. Considering that the recovery of the species in the Northern Territory started in severely depleted populations (Webb *et al.* 1984,

Webb *et al.* 1987) and much of their habitat, particularly extensive freshwater wetlands, remained relatively intact for recolonization (Webb and Manolis 1993a), it is plausible to assume that these populations are experiencing or have experienced exponential growth.

As a result, I included the exponential model in the set of hypotheses for *C. porosus* recovery pattern. The following two-parameter equation was taken from Crawley (2002).

$$y = be^{ax}$$

Where

y = crocodile density,

x = year since protection (1971),

e = natural logarithm,

a = population growth rate, and

b = initial population density in 1971.

The two models above assume indefinite increase of population as a function of time (the year since protection) that is obviously not the case in natural populations. Population growth is mostly limited by resources available in the environment (Stiling 2002). Natural populations usually show density-dependent dynamics, because constraints on the population growth become more severe as population densities become higher (Caughley and Sinclair 1994, Townsend *et al.* 2000). To take this into account, I introduced a logistic model that assumes that the rate of population increase decreases as the population grows and reduces availability of resources available in the environment at some point reaching an asymptote (Caughley and Sinclair 1994, Townsend *et al.* 2000, Stiling 2002). The asymptote, at which the growth rate becomes virtually zero, is defined as the carrying capacity of the environment to support the population (Townsend *et al.* 2000, Stiling 2002). This is an important feature of the model since the aim of this analysis is to examine the hypothesis that the populations are likely approaching carrying capacity. If the population data are adequately described by this asymptotic model, it will be an evidence for the hypothesis.

While the logistic model describes population growth more realistically than those that assume indefinite growth, the model has assumptions that limit its application to real populations. One of the most limiting assumptions is that rate of the production of the limiting resource is constant and independent of population size. Thus the population consumes only the production of the resource ('interest') but does not use nor damage the resource generating the production ('capital'). This is rarely met in natural conditions (Caughley and Sinclair 1994, Townsend *et al.* 2000, Stilling 2002). One of the few examples that met this assumption and thus showed the logistic population growth is wildbeest *Connochaetes taurinus* in the Serengeti of Tanzania and Kenya (Caughley and Sinclair 1994, Osborne 2000, Townsend *et al.* 2000). As they migrate to a seasonal supply of food and consume only the year's growth of grass, the population showed a kind of logistic growth. First, they exponentially increased from a low density caused by the disease rinderpest, and population growth was stabilized later with some fluctuations.

Despite the limiting assumption of the logistic model, Caughley and Sinclair (1994) pointed out that the application of the model is still useful in strategic modelling for qualitative aspects such as patterns or types, even when it is not entirely appropriate. They suggested that the model can be used confidently as a representative of models that assume limitation on population growth. Thus, the logistic model was considered appropriate in this analysis of population trends of *C. porosus* in the Northern Territory. This model was included in the set of the candidate models with most confidence as the recent studies on the crocodile population in the Northern Territory suggest (PWSNT 2004).

Among a number of different logistic models available, the following three-parameter logistic model was considered most appropriate due to the advantage of its simple form to predict an asymptotic trajectory and behaviour of the data (Crawley 2002).

$$y = c / (1 + e^{r(z-x)})$$

Where

c = carrying capacity,

r = intrinsic rate of increase, and

z = year since the protection (1971) with maximum growth rate
(the inflection point).

The three models for population growth described above are selected as a set of candidate hypotheses. Although all these models in the set have assumptions that may limit their application to the crocodile population data, it was not considered inappropriate because the information-theoretic paradigm does not expect any models that exactly represent full truth to be in the *a priori* set of models (Burnham and Anderson 1998; 2001; 2002). It does not even assume any such full reality can be parameterized (Anderson and Burnham 2002). The information-theoretic approach estimates the relative closeness of each fitted model to conceptual truth (Burnham and Anderson 2001) and the scope of this analysis is to find the model in the set that best approximate the crocodile population data.

The set of models were considered a appropriate size for the analysis as Burnham and Anderson (1998; 2001; 2002) suggest that the number of models in a set should be small, ideally a few models in which some *a priori* support exists. In addition, all the models have three or four parameters, which also agree with their recommendation for valid inference.

Having selected the set of *a priori* models, the crocodile population data were then prepared for the model fitting.

Crocodile population data

The historical crocodile population data for the Northern Territory were provided by WMI, PWSNT and PAN. These data in combination covered virtually all the survey years available in the rivers used in the previous analysis (Chapter 2) although the continuity and length of the years (sample size) differed for each river.

Although most of the major rivers were surveyed by spotlight, some small rivers had crocodile density data derived only from helicopter surveys. Those datasets with helicopter counts were excluded because data from the two different methods are not compatible without good deal of experimentation and manipulation (see Chapter 4) and more datasets were derived from spotlight surveys. Another main reason is that spotlight counts detect the sizes and numbers of animals more accurately than helicopter counts that are unable to recognize hatchlings (< 2 feet or 60.96 cm). Recognition of hatchlings was important because they were to be excluded from the analysis. This is because the abundance of hatchlings is highly variable depending on conditions for breeding and especially nest losses due to flooding, and its fluctuation tends to blur major trends in population changes (Bayliss and Messel 1990, Webb *et al.* 1998, Webb *et al.* 2000). Thus, crocodile densities would be calculated based on the numbers of animals larger than 2 feet.

From these spotlight-derived datasets, criteria for selecting rivers for the analysis were decided as follows; 1) rivers should have relatively uninterrupted sequences of samples to show more comprehensive trends in population growth, 2) they should also contain at least one survey on or after 2001 to provide the most recent population growth and 3) the set of rivers selected should cover a range of densities so that those population growth patterns would represent the full range of conditions encountered in the Northern Territory.

Using these criteria, five rivers were selected; the Tomkinson River with 25 years of data (1976-2003), the Liverpool River with 24 years (1976-2001), the Adelaide River with 21 years (1977-2002), the Daly River with 19 years (1978-2002) and the Mary River with 14 years (1984-2002). The first two rivers have the most continuous survey years and represent low to medium densities of crocodiles in the Northern Territory. The last three rivers also have a long history of survey since they are important monitoring sites with high crocodile densities (Webb *et al.* 1998, PWSNT 2004). The Tomkinson and Liverpool Rivers were treated as one dataset since these two rivers belong to the same river system, with the Tomkinson River connecting to the main stream of the Liverpool River (Figure 3.1). In addition, although there are some rivers with lower densities than the Tomkinson and Liverpool Rivers in the Gulf

of Carpentaria, they could not be included in the selection since none of them had recent spotlight counts. Specifications of the sections used for each river are presented below (Table 3.1).

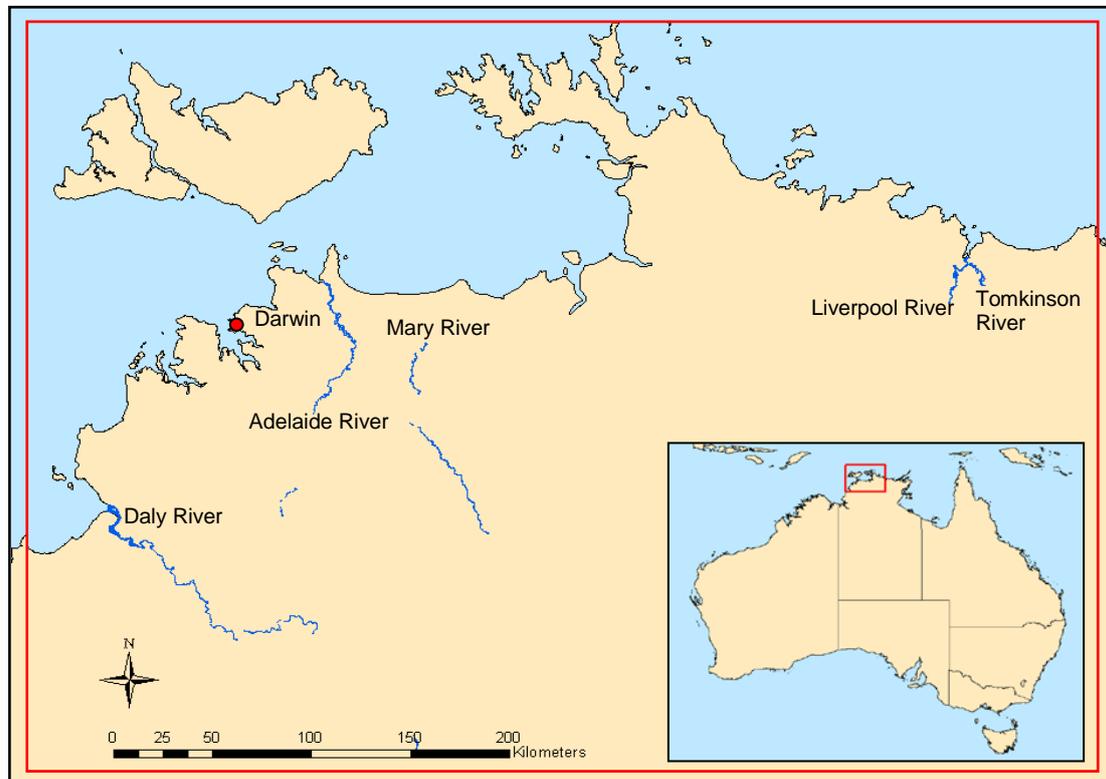


Figure 3.1. Map of the Northern Territory rivers selected for the analysis. Note that the Tomkinson River is a tributary of the Liverpool River in the same river system, thus they were treated as one river in the analysis.

Table 3.1. Specifications of the sections used for the density estimate calculation for each river. Local names are those in the crocodile data in the Northern Territory used by researchers. Start and End Points are starting and ending points of survey transects indicated by longitude and latitude in decimal degrees projected in the Geographic Datum Australia 94 (GDA 94). Those points for the Side Creeks of the Adelaide River are not shown since they are multiple small creeks connected to the mainstream, but they were included in the density calculation for the associated mainstream and its tributaries.

Rivers	River sections	Start Point		End Point	
Mary River	Mainstream	131.6369	-12.7132	131.6736	-12.7043
	Rockhole	131.6896	-12.7528	131.6510	-12.7516
	Hardies	131.5932	-12.7891	131.6307	-12.7900
	Corroboree Channel	131.6336	-12.7066	131.6435	-12.7113
	Downstream Bridge	131.6488	-12.9118	131.6415	-12.9050
	Mary (Sampan Creek Mouth - Alligator Lagoon Channel)	131.7787	-12.2648	131.7070	-12.2689
Liverpool/ Tomkinson Rivers	Liverpool Mainstream	134.2133	-12.0288	134.1026	-12.0205
	Morngarrie Creek	133.2293	-12.1238	133.2312	-12.1151
	Maragulidban Creek	134.1184	-12.1756	134.1026	-12.1692
	Mungardobolo Creek	134.1961	-12.1324	134.2040	-12.1421
	Tomkinson Main stream	134.1961	-12.1324	134.2783	-12.1421
Adelaide River	Mainstream total (0-117 km)	131.2346	-13.1221	131.2224	-13.1238
	Side Creeks	-	-	-	-
Daly River	Mainstream	130.7073	-13.7690	130.3088	-13.7622

Crocodile densities of these rivers were calculated as animal sighting per kilometre of river. In the calculation, there were some cases where data for individual sizes of crocodiles were not available. In spotlight surveys, if a spotted crocodile is submerged in the water with only eyes recognizable above the surface, it is often difficult for a spotter to estimate the total body length. In that case, they are recorded as ‘Eyes-Only’ in the dataset. These Eyes-Only data were included in the density calculation, according to Webb *et al.* (1998) that assumed that most Eyes-Only animals are wary animals larger than six feet long based on their calibration surveys in the Northern Territory rivers. Since the mean size of crocodile in populations increases in many of the Northern Territory rivers (Webb *et al.* 1998, PWSNT 2004), Eyes-Only animals are likely to be at least larger than two feet (thus, non-hatchlings) while it is difficult to estimate the general body size of Eyes-Only animals.

In addition, all population data for the Adelaide, Liverpool and Tomkinson Rivers in 1998 were excluded from the calculation because it was considered that they were not comparable with other years’ data. In 1998, some spotlight surveys were conducted at

high tide while all other surveys were done at low tide when more animals are visible (C. Manolis, pers. comm. WMI 2004, M. Letnic, pers. comm. PWSNT 2004).

Model fitting and selection

These density estimates of non-hatchlings in the selected rivers were then fitted into each of the candidate models, using the statistical software, R (version 1.9.1). In R, while the linear growth model was calculated as a linear regression, the exponential and logistic models were calculated as a non-linear regression via least squares. The least squares estimate the parameters of non-linear models by finding the parameter values that minimize the square of the deviations between the observed and fitted values in a model, with the restriction that the deviations follow a normal distribution (Dalgaard 2002). For this calculation, the software requires input of starting values for parameters to estimate the least squares. Considering the distribution of each dataset, different starting values were set until the algorithm converged on the data (e.g. $a = 0.5$ and $b = 0.1$ for the exponential model, and $c = 6$, $r = 0.5$, and $z = 17$ for the logistic model for the Mary River dataset).

In the model calculation, it was necessary to ensure that all the data were not overdispersed since overdispersion is a common problem in count data (Burnham and Anderson 2001, Anderson and Burnham 2002, Crawley 2002) and the crocodile densities were derived from counts in spotlight surveys. If data are overdispersed, it indicates that the estimated sampling variance is so small that the data may be somewhat dependent while a model may assume independence (Anderson and Burnham 2002). This in turn might imply that there is no valid information on any of the genuinely important parameters in the models (Crawley 2002). A simple approach to detect overdispersion is estimating a variance inflation factor (c) from a highly dimensioned model, using the following equation (Anderson and Burnham 2002, Crawley 2002).

$$c = rd / df$$

Where

c = variance inflation factor,

rd = residual deviance of a model, and

df = degree of freedom of the residual deviance.

If the variance inflation factor is larger than 1, it indicates that the data are overdispersed (Crawley 2002). Because overdispersed data require different approaches for model selection and inference (see below) (Anderson and Burnham 2002), it was important to examine whether the data are overdispersed. The variance inflation factor was estimated from the logistic model for each dataset since it has the most parameters in the set of models. All the variance inflation factors were smaller than 1, thus the datasets were not overdispersed.

The fit of the models for each dataset was examined using one of the Akaike's information criteria. Akaike Information Criterion (AIC) is one of the main components of the information-theoretic paradigm that is used to assess the relative performance of models (Burnham and Anderson 1998; 2001; 2002). AIC provides a formal link between the dominant paradigms of statistics and information theory by estimating the expected, relative Kullback-Leibler information (K-L information), based on the maximized log-likelihood function (Burnham and Anderson 2001). K-L information, often referred to as 'cross entropy' (Burnham and Anderson 2001), is a measure of distance between conceptual reality and the approximating model - the 'information' lost when a model is used to approximate reality (Burnham and Anderson 1998). AIC assesses the fit of a model to given data based on theoretical foundations of entropy, K-L information, and likelihood theory (Burnham and Anderson 2001). Thus, the smaller value of AIC indicates the better fit of a model with smaller loss of information. AIC is calculated using the following equation (Burnham and Anderson 2001, Crawley 2002).

$$AIC = -2 \times \log_e(L) + 2K$$

Where

$\log_e(L)$ = maximized log-likelihood, and

K = the number of parameters in the model.

Akaike Information Criterion (corrected) (AICc) is a small-sample version of AIC. This second-order AIC is used when the number of parameters is large or sample size (n) is small (Burnham and Anderson 2001). Anderson and Burnham (2002) suggest that AICc should be used instead of AIC if $n/K < \sim 40$. In this analysis, as n/K was 6 (the largest $n = 24$ in the Liverpool River dataset and $K = 4$ in the logistic model), AICc was calculated using the following equation (Burnham and Anderson 2001, Crawley 2002);

$$AICc = -2 \times \log_e(L) + 2K + (2K(K + 1) / (n - K - 1))$$

Where

n = sample size.

While AICc would need to be converted to another second order AIC (QAIC) in the case of overdispersion, it was not necessary since all the datasets were not overdispersed. As result, AICc values of each model were compared to identify the best-fitting model for each river.

Furthermore, the differences in AICc between the best-fitting model and other models in each river were calculated. This simple difference in AICc (or AIC) is expressed as Δ_i and useful for assessing the relative merits of candidate models in a set (Burnham and Anderson 1998, Burnham and Anderson 2001). Δ_i allows a quick comparison of 'strength of evidence' between hypotheses (models). Generally, if a model has Δ_i that is less than 2, the model has significant support (evidence), if Δ_i is between 4 and 7, the model is considerably less supported, and with a Δ_i larger than 10, there is essentially no support for the model compared to other models in the set (Burnham and Anderson 2001; 2002). These information criteria (AIC, AICc and Δ_i) provide a

practical methodology for rigorous, objective analysis of empirical data (Burnham and Anderson 2001).

The likelihood of each model was also estimated, using the simple transformation $\exp(-\Delta_i/2)$ for the model (Burnham and Anderson 2001). When these likelihoods of models in a set are normalized so that they sum to 1, they are called Akaike weights (w_i). The Akaike weight (w_i) for each model was calculated using the following equation.

$$w_i = \exp(-\Delta_i/2) / \text{sum of } \exp(-\Delta_i/2) \text{ for all models in a set}$$

The Akaike weights (w_i) are interpreted as ‘weight of evidence’ or an approximation of the probability that model is the actual K-L best model in the set (Burnham and Anderson 2001). In addition to AICc, the Akaike weights were used as another measure for ranking the models.

These model selection statistics under the information-theoretic approach were used to assess which of the three models best fit to each crocodile population dataset. Any null hypothesis tests and associated P -values were not used in the analysis since there is no relevance and linkage between the evidentiary information-theoretic paradigm and null hypothesis testing (Burnham and Anderson 1998; 2001; 2002, Anderson and Burnham 2002).

Based on the results of the model selection, estimates of the parameters in the model which was considered as best describing the population data were then compared between the rivers.

3.3. Results

The linear, exponential and logistic models were fitted into the selected rivers in the Northern Territory (Figure 3.2). While it proved possible to fit the linear and exponential models to all the rivers, the logistic model was not a good fit to the Liverpool / Tomkinson Rivers dataset (Figure 3.2.d). For unknown reasons, model

failed to converge on the dataset in a range of statistical packages (R, S-plus, and SAS).

The statistical results of the model selection under the information theoretic procedures for each dataset are provided below (Table 3.2-3.5). Each table contains the parameters that are argued necessary in any information-theoretic model selection by Anderson and Burnham (2002).

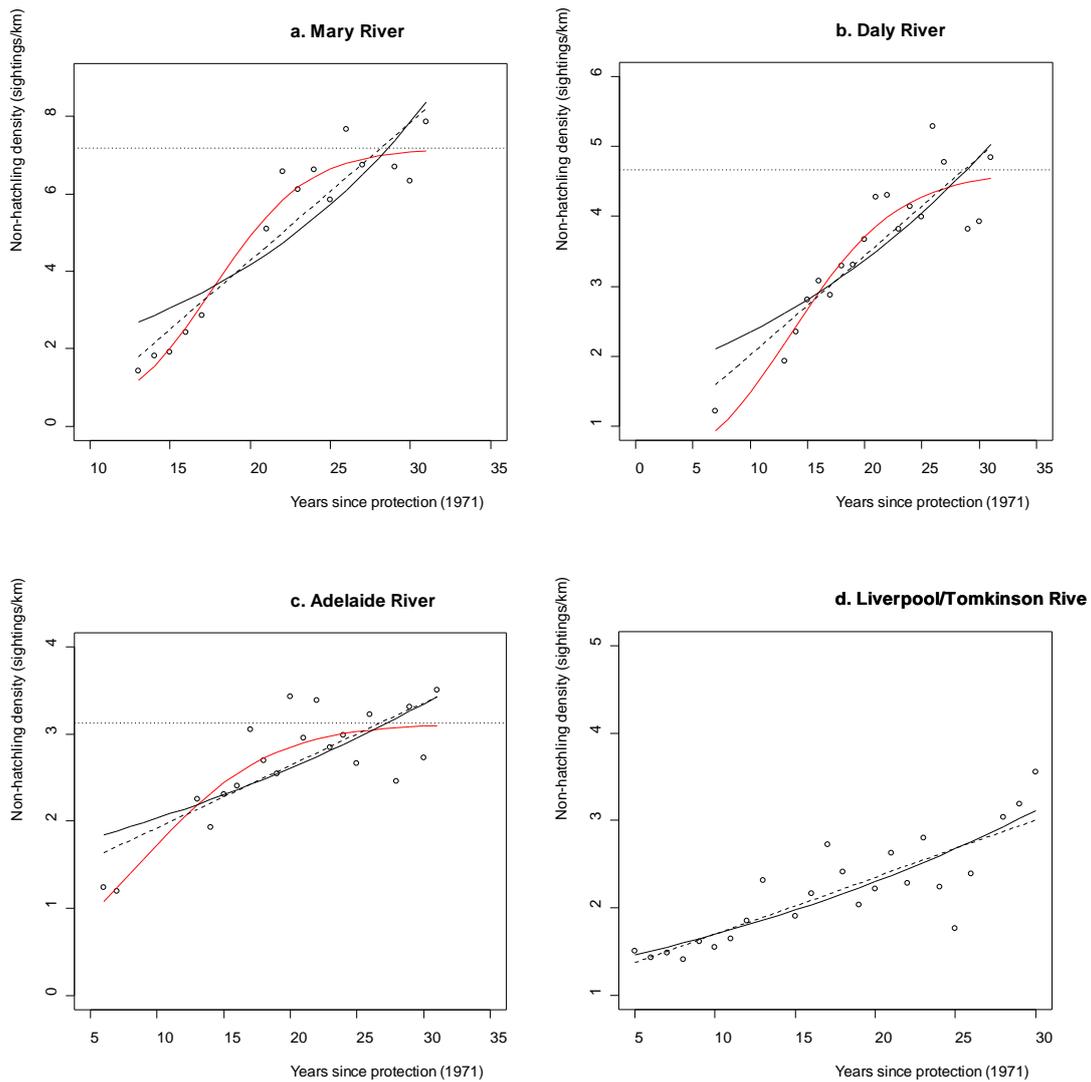


Figure 3.2. Density of *Crocodylus porosus* (sighting of crocodiles km^{-1}) in the Mary, Daly Adelaide, Tomkinson and Liverpool Rivers. The dashed line is the fitted linear model and the black solid line is the fitted exponential model, the red solid line is the logistic model with the predicted carrying capacity (asymptote) shown with a dotted line.

The Mary River showed much higher ‘strength of evidence’ for the logistic model than the exponential and linear models (Table 3.2). The logistic model had a higher maximized log-likelihood than the other two models. This is reflected in the other values of AICc and Akaike weights. The logistic model had a much smaller AICc than the linear and exponential models and their differences relative to the logistic model (Δ_i) were more than 10. These differences between the models are more highlighted by the Akaike weights; the Akaike weight of the logistic model was far higher than the other two, whose weights were marginal.

Table 3.2. Model selection statistics for the Mary River to estimate trends in population abundance of *C. porosus*. Notations; $\log_e(L)$ = maximized log-likelihood, K = number of parameters, AICc = Akaike information criterion corrected, Δ_i = difference in AICc, w_i = Akaike weight.

Model	$-\log_e(L)$	K	AICc	Δ_i	w_i
Linear	18.0	3	41.1	11.5	0.0026
Exponential	22.3	3	49.5	20.0	0.0001
Logistic	10.7	4	29.5	0	0.9973

The Daly River also showed strong support for the logistic model; the AICc was smallest with the logistic model and the largest was for the exponential model (Table 3.3). The value for Δ_i of the linear model was not as large as that of the exponential model. The Akaike weight of the logistic model was much larger than the others.

Table 3.3. Model selection statistics for the Daly River to estimate trends in population abundance of *C. porosus*. Notations; $\log_e(L)$ = maximized log-likelihood, K = number of parameters, AICc = Akaike information criterion corrected, Δ_i = AICc difference to minimum, w_i = Akaike weight.

Model	$-\log_e(L)$	K	AICc	Δ_i	w_i
Linear	12.8	3	30.4	6	0.047
Exponential	15.5	3	35.8	11.6	0.003
Logistic	8.4	4	24.4	0	0.950

The same trends as the Daly River were observed in the Adelaide River (Table 3.4). While the logistic model had the smallest AICc, that of the exponential was much higher than the other two models.

Table 3.4. Model selection statistics for the Adelaide River to estimate trends in population abundance of *C. porosus*. Notations; $\log_e(L)$ = maximized log-likelihood, K = number of parameters, AICc = Akaike information criterion corrected, Δ_i = difference in AICc, w_i = Akaike weight.

Model	$-\log_e(L)$	K	AICc	Δ_i	w_i
Linear	9.7	3	24.2	7.1	0.028
Exponential	11.2	3	27.2	10.1	0.006
Logistic	4.8	4	17.1	0	0.966

The Liverpool and Tomkinson Rivers showed different trends from all the other rivers (Table 3.5). While the logistic model did not converge, the linear and exponential models showed similar strengths of evidence to each other; the AICc difference between the two models was small and, thus their Akaike weights were also similar.

Table 3.5. Model selection statistics for the Liverpool and Tomkinson Rivers to estimate trends in population abundance of *C. porosus*. Note that the logistic model did not converge. Notations; $\log_e(L)$ = maximized log-likelihood, K = number of parameters, AICc = Akaike information criterion corrected, Δ_i = difference in AICc, w_i = Akaike weight.

Model	$-\log_e(L)$	K	AICc	Δ_i	w_i
Linear	6.2	3	17.0	0.6	0.433
Exponential	5.9	3	16.4	0	0.567
Logistic	-	4	-	-	-

In making inference based on a selected model from a set, estimates of precision due to the uncertainty about model selection should be included, unless there is strong evidence for the selected model such as an Akaike weight > approximately 0.9 (Anderson and Burnham 2002). One way to estimate precision is estimating sampling variance that is unconditional on any particular model but conditional on models in a set (Burnham and Anderson 2001). However, since the scope of this analysis is not any prediction using parameters of a model, but rather assessing fit of models, it was considered unnecessary to further calculate the unconditional sampling variance of each parameter across the logistic models, whose Akaike weights are more than 0.9.

Estimated values of the parameters in the logistic model differed between the Mary, Daly, and Adelaide Rivers (Table 3.6). The estimated carrying capacity (c) was highest in the Mary River while the Adelaide river showed the smallest carrying capacity. The intrinsic rate of increase (r) of the Mary River was also higher than the other two. The Daly, and Adelaide Rivers had the same intrinsic rate of increase. The

same trends to the carrying capacity were observed in the inflection point of the maximum growth rate (z).

Table 3.6. Estimated values of the parameters for the logistic model and their standard errors. c = carrying capacity, r = intrinsic rate of increase and z = year since protection with maximum growth rate (inflection point) and SE = standard error.

Dataset	c	SE	r	SE	z	SE
Mary River	7.19	0.33	0.34	0.06	17.74	0.61
Daly River	4.66	0.29	0.21	0.05	13.53	0.91
Adelaide River	3.13	0.16	0.21	0.06	9.01	1.22

3.4. Discussion

The results of the model selection showed strong evidence for the logistic model rather than the linear and exponential models in many rivers. Across the Mary, Daly, and Adelaide Rivers, the difference in AICc between the logistic and exponential models (Δ_i) were consistently large (> 10). According to the general rules of Burnham and Anderson (1998; 2001; 2002), a model with $\Delta_i > 10$ has ‘essentially no support’. The exponential model is clearly a poor fit to those rivers. The difference between the logistic and linear models was also more than 10 in the Mary River. The Δ_i of the linear model in the Daly, and Adelaide Rivers was in the range of 4-7, indicating that the model has ‘considerably less support’ (Burnham and Anderson 1998; 2001; 2002).

Moreover, the Akaike weights or ‘weight of evidence’ (Burnham and Anderson 2001) of the logistic model were strikingly high (> 0.9). Given that the Akaike weights are interpreted as ‘the probability that the model is the actual K-L best model in the set’ (Burnham and Anderson 2001), it is obvious that the logistic model best approximates these rivers’ data in the set.

On the other hand, the iterative numerical routine for the logistic model failed to converge on the Liverpool and Tomkinson Rivers. Failure to converge in the information-theoretic procedure is not unusual and it indicates that the computational routine cannot find the maximum of the log-likelihood (Anderson and Burnham 2002). There are many technical reasons for such failure (Anderson and Burnham 2002), and it is interesting that there was a failure to converge on the dataset in a range of statistical packages (R, S-plus and SAS). Bearing this in mind, it is difficult

to determine the trend in population abundance of these rivers, while there was similar support for the linear and exponential models.

In summary, the growth model that assumes an asymptote in population increase was most strongly supported in the set for the Mary, Daly, and Adelaide Rivers which span abundances varying more than two-fold. The predicted asymptotes of the logistic models are close to the observed contemporary densities in these rivers. This supports the hypothesis that a density-dependent slowing of growth (thus, population recovery) is well advanced. In addition, since these rivers are all major river systems spanning a good range of crocodile densities in the Northern Territory (Webb *et al.* 1984, Webb *et al.* 1998, Webb *et al.* 2000), the same type of trends may be observed in other rivers.

The Mary River showed higher estimates of the carrying capacity and intrinsic rate of increase than the other two rivers. This is consistent with the Mary River having consistently high densities of *C. porosus* throughout its history of survey since protection (Webb *et al.* 1990, Webb *et al.* 1992, Webb *et al.* 1998, Webb *et al.* 2000). Assuming that the Mary River is one of the most suitable rivers for crocodiles across northern Australia (Fukuda *et al. in press*), the intrinsic rate of increase of this river (0.34) is likely to be close to the maximum rate of increase of the species (r_{\max}) observed in wild populations.

The maximum rate of increase is the rate at which a population can achieve under fully optimum conditions (Peters 1983, Caughley and Sinclair 1994, Townsend *et al.* 2000). While the maximum rate of increase is rarely achieved in natural populations (Peters 1983, Caughley and Sinclair 1994), there are theoretical estimates of the maximum rate for a number of different organisms. Peters (1983) presented an equation relating the maximum rates of increase of a range of poikilotherms in relation to their body mass ranging from 10^{-10} to 1000 kg (Figure 3.3). These estimates show that, as the body mass of animals increases, their maximum rate of increase declines. However, assuming the intrinsic rate of increase in the Mary River as the maximum rate of increase of *C. porosus* in northern Australia, it seems that *C. porosus* has a much higher maximum rate of increase than 'average' poikilotherms.

The intrinsic rate of increase in the Daly, and Adelaide Rivers (0.21) is also higher than the maximum rate of increase of those poikilotherms.

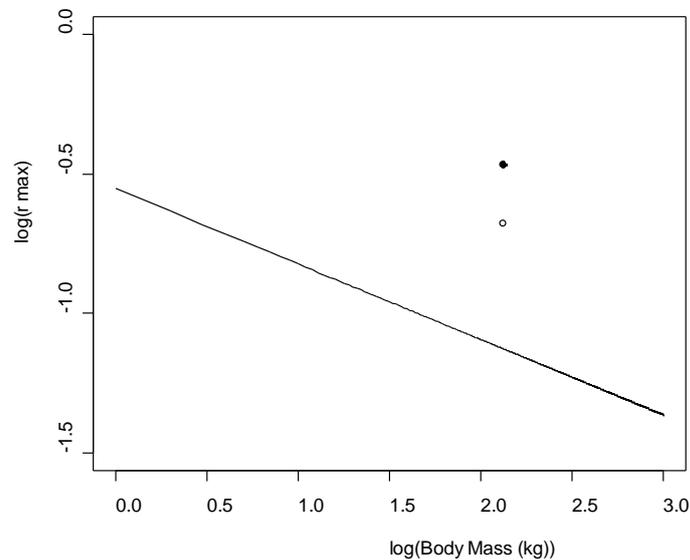


Figure 3.3. Relationship between the maximum rate of increase (r_{max}) and body size (kg) of poikilotherms (after Peters 1983). The r_{max} decreases as the body mass of animals increases. The filled point is the r_{max} of *C. porosus* in the Mary River (0.34) while the empty point is the intrinsic rate of increase in the Daly, and Adelaide Rivers (0.21). The body mass of *C. porosus* for these points is those of female crocodiles reaching at sexual maturity (total body length ~2.3 m) (Webb and Manolis 1993b). The body mass was calculated from the total body length as 133kg using conversion equation from Webb and Messel (1978).

Their high rate of increase may be explained by the biology of *C. porosus*. They have a relatively large clutch size of approximately 50 eggs per nest in the Northern Territory (Groombridge 1987, Cooper-Preston and Jenkins 1993, Webb and Manolis 1993a, Webb and Manolis 1993b). Although embryonic mortality is often high due to drowning from flooding, populations may increase rapidly, if hatchlings and juveniles achieve high survivorship. In the early stages of recovery, proportions of hatchlings and juveniles individuals were typically large in many rivers due to the removal by hunting of larger animals (Webb *et al.* 1998, PWSNT 2004). It is likely that the low densities of large individuals provided these small individuals some advantages such as more accessible resources and lower mortality, considering that the species shows cannibalistic behaviour, feeding on smaller individuals (Webb and Manolis 1988, Webb and Manolis 1993a, Webb and Manolis 1993b). In addition, once they reach sexual maturity at approximately 16 years for males and 12-14 years for females, their survivorship seems to be considerably higher (Webb and Manolis 1993a, Webb and

Manolis 1993b). Combining these features, the species may have potential for high fecundity.

A similar population growth is found in the wildbeest *Connochaetes taurinus* in the Serengeti (Osborne 2000, Townsend *et al.* 2000). Using the logistic model, Osborne (2000) estimated 0.28 to be the intrinsic rate of increase during their recovery from a rinderpest epidemic. This might be another example of a similar scenario to *C. porosus* in the Northern Territory.

In conclusion, I interpret these results of the model selection as further support that the recovery of *C. porosus* populations is now well advanced in most river systems of the Northern Territory and some are even reaching the carrying capacity. This, in turn, supports the hypothesis that rate of population increase is now being limited by the capacity of the environment to support crocodile populations. In other words, contemporary population density is likely to be influenced by the environment and their density-dependent interaction with their environment and each other more strongly than the impact from past hunting.

This outcome has two important implications for informative exploration of the species-environment relationship of *C. porosus* across northern Australia. First, it assumed that the situation is similar in Queensland and Western Australia after nearly 30 years of protection, we would expect that population abundances there are also related to environmental conditions. Second if recovery has been substantially suppressed in these States by either change in habitat condition associated with intensive agriculture or human population presence leading to direct destruction of crocodiles, then models incorporating indices of these features would be expected to be a better fit to the data on crocodile abundance across northern Australia than will models omitting such variables.

In short, if the past commercial hunting is no longer the dominant influence on the contemporary population abundance and it is the environment interacting with the internal dynamics of crocodile population, the key question is “What environmental factors are now most strongly influencing and making the differences in population abundance?” In the next Chapter, I will attempt to identify broad scale patterns of

variation in crocodile density and their relationships to environmental variables across northern Australia.

CHAPTER 4

Environment Influences on Contemporary Population Abundance across Northern Australia

4.1. Introduction

The comparison of population abundance estimates of *C. porosus* between the contemporary and pre-hunting period in the Northern Territory implied that the recovery of the contemporary populations from hunting has advanced to the level that those populations are now comparable to those before the hunting (Chapter 2). This historical comparison was further supported by the analysis of the patterns of change in population abundances in the same rivers (Chapter 3). Most rivers, particularly ones that now have large populations, showed clear evidence of a plateau in the rate of population increase. Based on these results, I concluded that the past hunting is no longer the dominant force limiting the contemporary population abundances; rather they are more likely to be reaching the carrying capacities, so that densities are strongly influenced by the quality of the environment associated with the rivers in which they were surveyed.

This leads to a new hypothesis that certain environmental factors are now determining those population abundances across northern Australia. If the environment is limiting those crocodile populations, it is necessary to consider the implications of standards of environmental management for population of *C. porosus* in northern Australia.

There has been a number of biogeographic studies that developed ecological models regarding the relationships between animals and the environmental features in their habitat. Anderson *et al.* (2002) developed a predictive model of habitat requirements of spiny pocket mice (*Heteromys australis* and *H. anomalus*) in South America based on topographic characteristics in known habitat. The model showed relatively high matching with observed distribution of the species. Bakker *et al.* (2002) built models to predict the distribution of passerines in North America. The models based on landscape structure that was quantified in a GIS recognized various distributions of different passerine species. Similar predictive models were developed to examine broad-scale influence of the environment variables, including both natural and

anthropological features, on the patchy distribution of great bustard in central Spain (Osborne *et al.* 2001). The model showed high agreement with census data while it also identified potentially suitable habitat that was not presently occupied. Wang *et al.* (2003) constructed a predictive model of species richness of bat in Mexico to examine the relationships between their distribution and environmental variables. Their results showed that their distributions were best characterized the variables of temperature, vegetation, precipitation and soil moisture.

The models in these studies were essentially developed to predict the occurrence or distribution of the species, based on the specific environmental features that are thought to influence the capacity of the species to occupy the habitat at any density. They depend strongly on comparing environmental features inside and outside of the species distribution. However, to examine the relationship between the environment and animal abundance rather than distribution, models at a different scale that examine relevant environmental features within the range of their distribution are required. This chapter provides such an analysis within the range of *C. porosus* in north Australia.

The aim of this analysis is to 1) examine the relationships between the contemporary population abundance of *C. porosus* and the environmental features in their habitat and 2) determine whether natural environmental variables or human-impact variables are more likely to be influencing crocodile abundance.

To examine the abundance-environment relationships of *C. porosus*, this analysis uses the information theoretic approach in which hypotheses about the relationships are first formed based on the biology and ecology of the species, the hypotheses are framed as models and the evidence in support of each model is estimated to compare to other models.

4.2. Methods

Crocodile population density

This analysis was conducted on catchment basis to model the relationship between population abundance of *C. porosus* and the environment across northern Australia. The abundance of crocodiles across northern Australia was regarded as a response variable to various environmental factors as explanatory variables. The crocodile abundance was derived from contemporary population data collected in extensive surveys in rivers conducted by a number of organizations. Since most of the population data are based on river systems, whose properties and characteristics are affected by a number of environmental factors in a whole catchment (NLWRA 2004), catchments were considered an appropriate scale for the modelling.

However, some catchments as they defined by Geoscience Australia needed to be further divided because they contained more than two unconnected river systems and each of them has crocodile population data. As long as each of rivers in the same catchment contains crocodile population data and these rivers are independent of each other as different river systems in terms of topography, it was considered appropriate to treat them as separate samples for the analysis. Thus, catchments with those rivers were separated into sub-catchments based on topography (Digital Elevation Model (DEM)).

The measure of the response variable was first determined. As a more relevant representation of crocodile densities in catchments or subcatchmentss, density in biomass (kg) of crocodiles per km of rivers was considered an appropriate indicator of animal abundance rather than traditional density in sighting of crocodiles per km of rivers. Body sizes of the species are highly variable ranging from approximately 0.1 to 1000 kg (Webb and Manolis 1993b). The biomass density provides a measure that takes account of the variation in size structure of populations and reduces risk of bias by highly variable counts of small individuals. Thus, the biomass density was used for this analysis, unlike the previous analyses where density estimates based on the number of individuals sufficed for the aims of study. Description of the crocodile population data obtained and calculations of the density estimates are provided below.

a. Northern Territory

The crocodile data for the Northern Territory were provided by Wildlife Management International, Parks and Wildlife Service of the Northern Territory, and Parks Australia.

With a few exception in lakes and billabongs, most of the crocodile data come from surveys in certain sections of river systems, consisting of a mainstream and side creeks. In the Northern Territory, those river sections cover much of the species' distribution.

First, crocodile population data collected in spotlight surveys were extracted because while some small rivers have helicopter surveys, most of major rivers have been covered by spotlight surveys and spotlight survey data can recognize the size of animals with more precision. A total of 19 datasets with spotlight counts were obtained. From these datasets, the most recent data for each river were further extracted. The most recent years where the data are available differed among the rivers (Table 4.1).

Table 4.1. Crocodile datasets of rivers with spotlight counts and their most recent years in the Northern Territory.

River	Year
Adelaide River	2002
Moyle River	2002
Daly River	2002
Mary River	2001
Victoria/Baines River	2001
Liverpool River	2001
Baralminar/Gobalpa River	2000
Goromuru River	2000
Habgood River	2000
Cato/Peter John River	2000
Blyth River	1999
Roper River	1999
Wildman River	1998
West Alligator River	1998
South Alligator River	1998
East Alligator River	1998
Glyde River	1997
Finniss River	1995
Reynolds River	1995

However, there were sometimes situations where surveyed river sections differed among years in a river system – some years had more surveyed sections than did other years within the same river. For example in, the Mary River dataset in 2002, the most recent year available consists of 6 sections while 2001 dataset has 8 sub-datasets. In this case, the 2001 dataset was chosen to characterize the Mary River catchment. Selection for the most complete dataset rather than the most recent was considered appropriate to characterize a catchment or subcatchment since the previous population analyses concluded that contemporary population densities are nearing saturation, or at least have stabilized in many rivers of the Northern Territory. Hence, the most complete datasets were selected as long as they are not too old (usually the second most recent year's data) if the most recent datasets were not most complete (Table 4.1).

While the most recent year available in the datasets may vary among catchments and subcatchmentss I ensured that all data from different river sections within the same catchment came from the same year to retain data compatibility within each catchment or subcatchment.

All crocodile datasets in the Northern Territory are conventionally formatted in a consistent style in which the number of crocodile sighting is summarized in classes of total body length estimates (in one foot or 30 cm increments), ranging from hatchling (< 2 feet) to > 17 feet. When size estimation was not possible in spotlight surveys, those animals were recorded as Eyes-Only.

For the calculation of crocodile biomass, conversion coefficients were derived from a morphometric study by Webb and Messel (1978). They collected morphometric measurements from 1354 *C. porosus* captured in the north coast of Arnhem Land and developed a series of formulae for predicting morphometric attributes from one another, such as predicting snout-vent length from total body length and body weight, or vice versa. Assuming that animal's morphology would not differ greatly among regions across northern Australia, those coefficients were used for the data conversion.

First, total body length estimates in the datasets were converted to snout-vent length. Total body length was assumed to be the median of each class (e.g. crocodiles in 3-4 feet class were assumed to be 3.5 feet-long). Regression intercept and coefficient for snout-vent length varied depending on total body length (divided in three classes of 25-85, 85-260, 260-425 cm). Predicted snout-vent lengths were then converted to body weights.

The conversion was possible only up to 13.5 feet class since the coefficients of Webb and Messel (1978) do not recognize animals larger than 425 cm (13.9 feet) due to unavailability of large animal samples at the time of study. Conversion coefficients for individuals larger than 425 cm were, however, required as some of the datasets contained individuals in 14.5 and 15.5 feet classes.

To obtain coefficient in those classes, the predicted values of biomass in the available classes were first imported and plotted in the statistic package, R (version 1.9.1) (Figure 2).

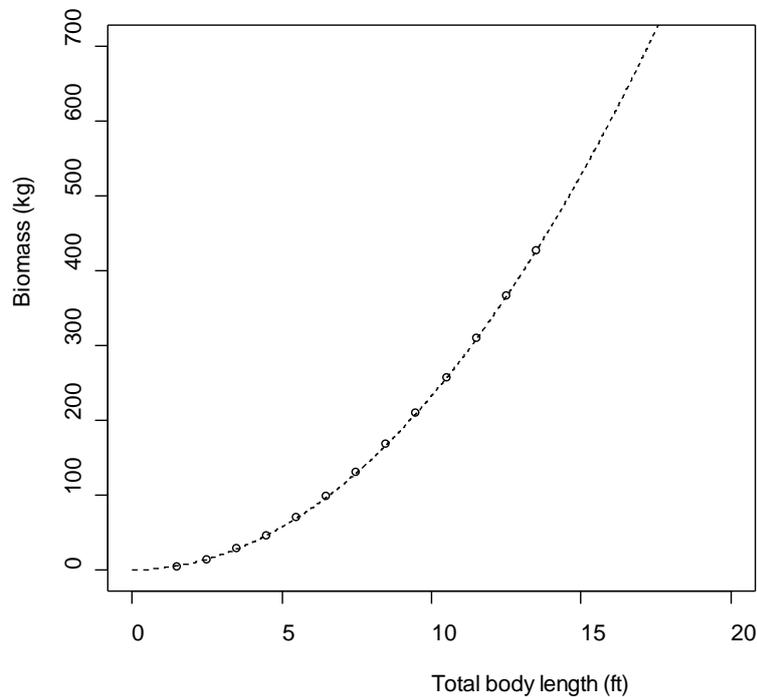


Figure 4.1. Predicted biomass of *C. porosus* at total body lengths ranging from 1.5 to 13.5 feet. The dotted line is the fitted regression model (power).

The biomass values increase rapidly as a function of total body length. Those values were fitted into two-parameter power function as a non-linear regression model as follows:

$$B = aT^b$$

Where

B = biomass (kg),

T = total body length (feet).

The power function model fitted well (Figure 4.1) and provided estimates for the two parameters as $a = 2.19$ with standard error of 0.027 and $b = 2.03$ with standard error of 0.004. This equation was used to predict biomasses at 14.5 and 15.5 feet (Table 4.2).

Table 4.2. Predicted snout-vent length and body weight from total body length. TBL = total body length, SVL = snout-vent-length and TBW = total body weight. Note that predictions for total body weight at 14.5 and 15.5 feet were calculated based on the predictions at the shorter total body lengths derived from Webb and Messel (1978).

TBL (ft)	SVL (cm)	TBW (kg)
1.5	21.67	4.23
2.5	36.30	12.15
3.5	51.40	27.41
4.5	66.34	45.91
5.5	81.27	69.15
6.5	96.21	97.14
7.5	111.14	129.88
8.5	126.08	167.36
9.5	141.16	210.03
10.5	156.10	257.05
11.5	171.03	308.81
12.5	185.97	365.32
13.5	200.91	426.57
14.5	-	498.91
15.5	-	571.24

Another aspect of datasets that needed to be considered in biomass conversion were the Eyes-Only observation. Although total body lengths for Eyes-Only animals are unknown, some generalization may be possible based on much local knowledge of survey area and experience in spotlight surveys. Webb *et al.* (1998) estimated that crocodiles recorded as Eyes-Only would be larger than 6 feet in reality based on calibration surveys of spotlight and helicopter counts from 1984 to 1986 in the

Northern Territory. However, without local knowledge and sufficient experience in all the surveyed regions across northern Australia, it was difficult to make generalizations for each different river. I joined an annual spotlight survey conducted by Parks and Wildlife Service of the Northern Territory to detect *C. porosus* in some sections of the Adelaide and the Mary River in 2004. Throughout those surveys, my observation was that Eyes-Only animals could be any size from hatchling to large individual when the first spotter observed them as Eyes-Only and the second spotter estimated their sizes with more confidence. Rather than involving potential bias in relying on generalizations about Eyes-Only data, I assumed that Eye-Only sighting could fall in any class in the possible range of total body length from 1.5 to 15.5 feet. Because crocodile population structure in size is hierarchy with fewer individuals at larger sizes (PWSNT 2003), proportions of each size class were taken from some rivers so that each Eyes-Only sighting would be assigned their total body length according to the proportions of those representative rivers. The Adelaide, Mary, and Daly Rivers were selected as they have large number of sightings ranging from 1.5 to 15.5 feet classes.

Now total biomass of crocodiles in each size class, including Eyes-Only class, was calculated by multiplying the biomass at the estimated total body length by the number of animals within each class. Then, those total biomasses were summed and divided by survey distances to calculate crocodile density in biomass (kg per km) of river for each catchment or subcatchment.

b. Queensland

Crocodile population data in Queensland were provided by Queensland Parks and Wildlife Service. They consist of a number of datasets in different rivers and all the data were collected in spotlight surveys.

The most recent datasets were extracted from each river, ranging from late 1990s to 2000s. Although the most recent years available differed among catchments and subcatchmentss and many of them have more than one river system, all datasets in the same catchment or subcatchment had the most recent year in common (Table 4.3).

Table 4.3. Crocodile datasets of rivers with spotlight counts and their most recent years in Queensland.

River	Year
Wenlock River/Wenlock/Tentpole/Hudson Creeks	2003
South/North Brancj Mission River	2003
Normanby/Kennedy/Bizant Rivers	2003
Embley/Hey Rivers/Liethen/Triwall Creeks	2003
Andoom Creek	2003
South Edward River/Balurga Creek	2001
North Mitchle/South Mitchel River	2001
Mungkan Creek	2001
Coleman River	2001
Chapman River	2001
Trinity Inlet	2000
Russel River	2000
Pascoe River	2000
Packers Creek	2000
Olive/Kangaroo Rivers/Glennie Creek	2000
Mulgrave River	2000
Lockhart River	2000
Hull River	2000
Haughton River	2000
Harmer Creek	2000
Escape River/Jacky Jacky Creek	2000
Endeavour River	2000
Daintree/South Daintree Rivers/Saltwater Creek	2000
Cowal Creek	2000
Barron River	2000
Staaten River	1999
Proserpine River	1999
Norman River/Six Mile/Walkers Creeks	1999
Nicholson River	1999
Albert River	1999
Bohle River	1998
Alligator River	1998
Murray River	1997
Meunga Creek	1997

Unlike the Northern Territory datasets in which numbers of crocodile sighting are summarized in each size class, the Queensland datasets take records of each crocodile sighted in the spotlight surveys. This data format affords recognition of sighting details such as habitat and Global Positioning System (GPS) location as well as total body length of each individual.

However, lengths of rivers surveyed that are necessary for crocodile density calculations were not specified in the datasets. To obtain the survey distances for each

river, crocodile sighting points with GPS reading in the datasets were plotted in a GIS. Those sighting points were overlaid with topographic mapping layers of water bodies, catchments and subcatchments (TOPO 250K: Hydrography Theme, Australian Surface Water Management Area 2000, Nested catchments and sub-catchments for the Australian continent). For accurate measurement for river distances in metric system, all the layers were projected in the Map Grid of Australia (Datum: GDA 94, Projection: Universal Transverse Mercator). In the Universal Transverse Mercator system (UTM), some catchments and subcatchments are often laid over two different UTM Zones. In this case, they were projected into the Zone in which more area of a catchment or subcatchment is contained. Each survey section in most of the rivers had starting and ending points of spotlight survey transection, and distance between those two points were measured along topography of the rivers. In the case that a complete set of these points was not available, crocodile sighting points at the either ends of a transect were taken as starting or ending point of the survey after consultation with the researcher who had conducted the surveys.

Then, all the numbers of the crocodile sighting in each river were summarized into the total body length classes that were consistent with those used for the Northern Territory data.

As in the datasets for the Northern Territory, all Eyes-Only animals were assumed to fall in any size class and their total body lengths were derived from proportions of a few representative rivers in Queensland. The Wenlock, Normanby and Proserpine Rivers were selected for proportion sampling since they had relatively large numbers of crocodiles are a wide range of total body length.

Total numbers of crocodile sighting in each total body length were then converted into biomass using the conversion factors previously described (Table 4.2). Densities in crocodile biomass (kg per km) of surveyed river were calculated for each catchment or subcatchment in Queensland.

c. Western Australia

Crocodile population data for Western Australia were provided by Western Australia Department of Conservation and Land Management through Wildlife Management International.

Unlike other datasets in the Northern Territory and Queensland, most of the Western Australia crocodile datasets consist of helicopter survey counts. Among several rivers currently surveyed in Western Australia, the King River is the only river where spotlight survey has consistently been conducted up to 2003. Although spotlight surveys were also used for the other rivers in the late 1970s and 80s, helicopter survey has now replaced spotlight survey in those rivers. Data from helicopter surveys cannot be directly compared with spotlight data because helicopter surveys usually recognize fewer crocodiles due to limited visibility of crocodiles from a helicopter.

However, the helicopter data in Western Australia can be converted to corresponding spotlight count indices or *vice versa* by calculating the ratio between helicopter and spotlight counts (WMI 1992, CALM 2003). The ratio calculation is possible only if both helicopter and spotlight surveys are carried out at the same time, covering the same portion of the surveyed rivers. The Western Australia Department of Conservation and Land Management, and Wildlife Management International conducted both helicopter and spotlight surveys along the same distance in all the surveyed rivers in 1992 so that helicopter indices could be readily converted to spotlight counts.

Despite variation in crocodile population abundance (Bayliss and Messel 1990), it is likely that efficiencies in helicopter and spotlight counting remains constant as long as same method is followed (Bayliss 1987). If the relationship between helicopter and spotlight counts remains unvaried over time due to the fixed survey methodology, the ratio between helicopter and spotlight counting derived in 1992 is likely similar in later years. In addition, although it is argued that visibility of crocodiles may be subjective and varying among different observers, the crocodile data in 1992 and 2003, the most recent year for all the rivers, were collected by the same spotters (employed by WMI). Therefore, I assumed that use of the conversion ratios derived

from 1992 data would still be valid in 2003 data and introduce no bias into the calculation.

In addition, the helicopter datasets usually refer to crocodile counts only on one bank of a river while the spotlight datasets are based on both sides. The conversion of helicopter are done to refer to both sides of a river, making them compatible with other spotlight datasets in the Northern Territory and Queensland.

Ratios of helicopter counts to spotlight counts were then calculated for each dataset to convert the helicopter counts to spotlight relevant counts (Table 4.4). While most rivers were assigned an individual ratio based on its data, the Patrick River and the Parry Creek were exceptions where the ratio calculation was not possible. In the Patrick River, there was no crocodile sighting in the spotlight survey in 1992 so that the helicopter/spotlight count ratio could not be calculated. The Parry River had different surveyed distances between helicopter and spotlight surveys in 1992 (12 km in helicopter survey and 13.5 km in spotlight). However, WMI (1992) calculated mean helicopter/spotlight ratios separately for the West Arm and the Ord River regions so that any river in the Cambridge Gulf can use either of the two ratios even if the calculation is not possible for the area. Since both the Patrick River and the Parry Creek are side creeks of the West Arm within the same catchment or subcatchment (the Pentecost River), the mean ratio for the West Arm region was used for those two rivers. Total number of crocodile sighting in each helicopter dataset was converted to spotlight index, using these ratios.

Table 4.4. Western Australian rivers and their ratios of helicopter to spotlight counts for data conversion from helicopter to spotlight relevant indices. Local names are those used in the consist format for crocodile data in Western Australia. NB, SB, EB, and WB = north bank, south bank, east bank, and west bank respectively in helicopter survey. Note that helicopter counts are based on one or two sides of rivers while spotlight counts refer to all banks of rivers so that it will be compatible to other spotlight data in the Northern Territory and Queensland. The ratios for the Patrick River and the Parry Creek are the mean ratio for the West Arm region derived from WMI (1992).

Local name	HC/SC Ratio
West Arm mainstream 0-62 km (EB+SB)	0.483
Forrest River (NB)	0.333
Durack River (NB)	0.571
Pentecost River (WB)	0.214
Ord River mainstream 20-80km (EB)	0.421
Patrick River (WB)	0.355
Parry Creek (SB)	0.355

Helicopter data format also differs from that of spotlight survey in estimating total body length of animals sighted. Because of the greater distance of a helicopter from a crocodile during survey, helicopter surveys have been standardized to recognize only 4 classes for total body length (small: 2-4 feet, medium: 4-7, large: 7-11, and extra large: >11) while spotlight data record size classes in 1 foot (30 cm) increments ranging from <2 to >17 feet.

However, it was necessary to reclassify all the converted datasets into the spotlight relevant size classes so that biomass of each size class could be calculated. For reclassification, it was assumed that there would have been similar proportions of crocodile sighting at each class of total body length to those of the King River since it is the only river where actual spotlight data are available in Western Australia. Thus, the number of crocodile sightings in each spotlight relevant class was predicted by multiplying the total number of crocodile sightings in a dataset converted from helicopter to spotlight by the proportions at each class in the King River.

Total body lengths of The Eyes Only data in the King River were predicted from proportions of each size class of the river as it was the only spotlight-surveyed river.

Since the smallest class of total body length that helicopter surveys can reliably detect is 4-7 feet, hatchlings are not included in the datasets originally derived from helicopter surveys. However, in the Cambridge region where the population data are

available in Western Australia, all the rivers – including the ones surveyed by helicopter originally – have little *C. porosus* breeding due simply to limited nesting sites (Burbidge 1987, McNamara and Wyre 1994, CALM 2003). Because of limited breeding, the number of animals in the hatchling class (>2 feet) is likely small in those rivers. Moreover, those small numbers of hatchlings will have little influence on calculation of total biomass. For example, although the King River is one of the few rivers where successful nesting may be observed in the Cambridge region (CALM 2003) and the river had a high proportion of hatchlings (40.1% in total number of sightings) in 2003, the proportion becomes much smaller in biomass (10.0% in total crocodile biomass). Therefore, I assumed that biomass figures calculated from the datasets originally derived from helicopter survey are reasonably comparable with those from spotlight surveys.

Total crocodile biomass in each river was then summarized on a catchment or subcatchment basis to calculate crocodile densities in biomass (kg per km of river). Although rivers and their creeks usually fall into closed catchments or subcatchments, the West Arm lies on a boundary of two different catchments (Ord River and Pentacost River). However, it was assigned to the Ord River catchment since its original helicopter survey was conducted along the south and east banks of the river that belongs in the Ord River catchment.

Across the Northern Territory, Queensland, and Western Australia, the contemporary population densities in biomass (kg/km) could be estimated for a total of 55 catchments and subcatchments (19 for the Northern Territory, 24 for Queensland, and 2 for Western Australia).

Environmental data

Having prepared the population densities as the response variable at the catchment and subcatchment scale, I identified available datasets of the environment that were considered relevant to prospective explanatory variables.

A GIS dataset of catchments, Australian Surface Water Management Area 2000 (SWMA) was derived from Geoscience Australia. This is a vector dataset consisting

of catchments and river basins at scales ranging from 1:50 000 to 1:25000 across Australia.

Another GIS dataset of subcatchment, nested catchments and sub-catchments for the Australian continent was derived from the National Land and Water Resources Audit (NLWRA). It was developed by the Centre for Resource and Environmental Studies (CRES) at the Australian National University, based on Version 2 of the 9-second continental Digital Elevation Model (DEM) at 1:1000 000 scale.

Another GIS dataset for national hydrology, Geodata TOPO 250K Series 2: Hydrography Theme (TOPO 250K) was obtained from Geoscience Australia. This dataset contains vector data of various types of waterbody and related features in polygons at the scale of 1:25000.

Another GIS dataset, Global Map Australia 1M 2001 (GMA 1M) was obtained from Geoscience Australia. This comprehensive dataset is a set of vector and raster data at 1:1000 000 scale. The vector data include boundaries, drainage, population centers, and transportation while the raster data include elevation, land cover, landuse, and vegetation.

A dataset of elevation, version 2 of the 9-second continental DEM was obtained from Geoscience Australia *via* the Tropical Spatial Science Group at Charles Darwin University. It comprised raster grids at the scale of 1:250 000, consisting of several tiles to cover different regions across northern Australia.

Another GIS dataset for vegetation data, the Vegetation Communities of the Tropical Savanna (VCTS) was obtained from the Cooperative Research Centre for Tropical Savannas Management (CRC) *via* the Key Centre for Tropical Wildlife Management at Charles Darwin University. This vector dataset contains distribution and description of over 120 vegetation communities in tropical savanna across northern Australia at the scale of 1:1000 000.

However, this dataset covered only the tropical savanna regions in northern Australia, missing data for the Queensland Wet Tropics and Central Coastal regions. The

vegetation data for these regions was derived from another data source, the Survey and Mapping of 2001 Remnant Vegetation Communities and Regional Ecosystems of Queensland (RVCQ 2001) provided by Queensland Herbarium, Environmental Protection Agency. This detailed vegetation map was vector data at the scale of 1:100 000 and 1:50 000 in part, based on surveys of vegetation communities.

As a data source of climate, ANUCLIM (version 5.1) was obtained. It is a software package developed by CRES, Australian National University for calculating synthetic estimates of climate variables and bioclimatic parameters, using mathematical descriptions called climate surfaces. The climate surfaces are generated from long-term monthly averages of the climate variables at numerous station points across Australia (CRES 2000).

For water salinity data, a series of the Monographs (Messel *et al.* 1979-1987) were obtained. It is a series of reports, summarizing the results of the crocodile surveys conducted in major rivers across the Northern Territory, and parts of Queensland and Western Australia. Other than crocodile population data, it includes water salinity profiles and temperatures in the surveyed rivers.

Since the Monographs do not cover all the rivers of this analysis, two hydrological databases were accessed. The first database was National Resource Atlas developed by National Land and Water Resources Audit. This database includes a number of parameters of water properties of rivers including salinity. However, it did not include many small rivers in northern Australia, especially for water salinity measurement. The second database was OzEstuaries developed by GeoScience Australia as part of contribution to National Land and Water Resources Audit and Cooperative Research Centre for Coastal Zone, Estuary and Waterway Management. While it does not include direct measure of water salinities, the database contains broad geomorphic conceptual models that classify estuaries and waterways into various coastal waterway classes based on the structure, evolutionary characteristics and geomorphology of each waterway (Geoscience Australia 2004).

A GIS dataset, Indicators of Catchment Condition in the Intensive Landuse Zone of Australia – Feral Animal Density was also obtained from Australian Natural Resource

Library. This is a grid map of feral animals density on catchment basis at a scale of 1:25 000 000. However, the data did not cover much of eastern areas in the Northern Territory.

For data on land use across northern Australia, '1996/97 Land Use of Australia, Summary Interpretation for the Australian Natural Resources Atlas (NLWRA), National Land and Water Resources Audit' was obtained. This comprises raster grids of land use at the scale of 1:1 000 000 and provided from the NLWRA via the Weed Branch, the Northern Territory Department of Infrastructure Planning and Environment. The dataset contained a number of different land uses over the Australian continent.

For human demographic data, the 2001 Census of Population and Housing was obtained from Australian Bureau of Statistics. This includes demographic parameters for cities, towns, and local communities across northern Australia.

Data on crocodile harvesting were obtained from the PWSNT for the Northern Territory, and CALM for the Western Australia. These data were provided as Government reports with detailed information on crocodiles harvested in recent years. However, the same data were not available for Queensland.

Hypothesis building

I identified the following environmental factors as most likely to be influencing the abundance and distribution of *C. porosus* in Northern Australia, based on the scientific literature and other information on the biology and ecology of the species. While many environmental variables were possible, I have selected a relatively small range of variables to avoid the 'data-dredging' syndrome that might generate spurious conclusions with no valid ecological interpretation as warned by Burnham and Anderson (1998; 2001; 2002). A measure of each variable was also selected such that it would effectively capture the ecological and biological importance of the feature and it also could be derived from the available datasets. Description of each environmental variable and rationale of the selection are provided below.

1. Temperature

As a fundamental determinant of the species distribution, temperature was first considered. *C. porosus* distribution is restricted to tropical and subtropical regions of the world while alligators such as American alligator (*Alligator mississippiensis*) are found in habitat where temperature decrease below 0°C in the winter (Groombridge 1987, Grigg and Gans 1993, Webb and Manolis 1993b). The relationship between *C. porosus* and temperature is obviously an important factor determining their distribution and abundance in the wild although much detail is still left unknown (Taplin 1987, Webb 1991, Cooper-Preston and Jenkins 1993, Webb and Manolis 1993b, Miller 1994, PWSNT 2003).

As heterotherms, the effects of ambient temperature on their behaviour and physiology are striking. In the dry season, the cool temperature enhances more basking on banks and restricts their feeding and growth (Webb 1991, Cooper-Preston and Jenkins 1993, Grigg and Gans 1993, Molnar 1993). It also restricts their mobility with the body temperatures, except for large individuals, usually at or near ambient water temperature (around 25-28 °C) for *C. porosus* in northern Australian estuaries (Grigg and Gans 1993). Rates of body temperature increase is controlled by thermal time constant that is largely affected by their body mass such that body temperature rises and decrease faster in small individuals than large ones (Lang 1987a, Grigg and Gans 1993). Developing temperature in the early wet season then start stimulating their feeding and mobility (Webb 1991). Active animals commonly attain higher body temperature between 30-33 °C (Grigg and Gans 1993).

Temperature also seems a critical determinant for breeding as well as feeding and movement. Webb (1991) summarized potential influences of season on crocodile populations in northern Australia with a particular emphasis on breeding and nesting. Variable temperature and water level are proposed as two factors likely to determine the timing and extent of nesting. Rapid increase in the temperature in the late dry season to the early wet season (August to November) seems to trigger reproductive activities of crocodiles. Talpin (1987; 1990) and Miller (1994) argue that the relatively cold temperature in the dry season in Queensland limits much growing and reproductive opportunities. Thus, the minimum temperature experience during an

annual cycle strongly influences the distribution and abundance of breeding populations. The minimum temperature also seems to effectively distinguish favourable coastal regions within approximately 100km of the sea across northern Australia (Figure 4.2).

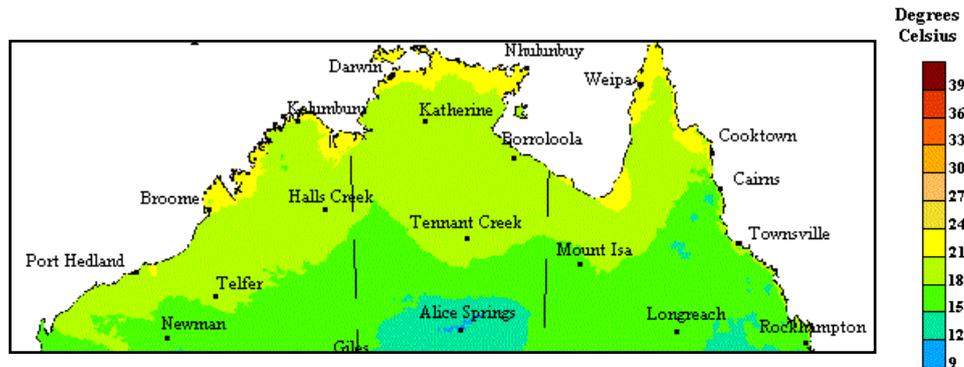


Figure 4.2. Average annual minimum temperature in northern Australia based on a standard 30-year climatology (1961-1990) (Modified from Bureau of Meteorology 2004).

While a number of different variables are possible on this aspect, the mean temperature in the coldest quarter of a year was considered appropriate in terms of the scale to capture this fundamental environmental requirement for suitable habitat.

2. Vegetation

In the Northern Territory, freshwater floodplains and swamps with tall sedges and grass are often associated with rivers with very high crocodile density (Webb *et al.* 1987, Webb 1991, Webb and Manolis 1993b). Webb and Manolis (1993b) speculated that heavily vegetated billabongs and swamps contain perhaps half of the total crocodile population in the Northern Territory while the other half are distributed in tidal waterbodies. Vegetation is also important for nesting in both total freshwater and tidal habitats (Groombridge 1987, Webb *et al.* 1987, Webb 1991, Cooper-Preston and Jenkins 1993, Fukuda *et al.* in press). Small monsoonal forests and swamp patches dominated by reed, sedge and melaleuca with freshwater spring on floodplains are the most important nesting sites in the Northern Territory (Webb *et al.* 1987, Webb 1991, Webb and Manolis 1993b). Floating rafts of vegetation are also common nesting sites in freshwater billabongs and swamps (Webb and Manolis 1993a.). Although tidally inundated mangrove swamps are rarely used for nesting, slightly elevated grass plains behind mangrove fringe are another favoured nesting site in the Northern Territory

(Webb 1991, Webb and Manolis 1993b). Contradictorily, most habitats in the Kimberley of Western Australia include much rugged rocky country with very few freshwater swamps and floodplains (Burbidge 1987, Mawson *in press*). The limited availability of suitable riparian vegetation may result in low breeding in the region (Burbidge 1987, CALM 2003, Mawson *in press*).

The favourable vegetation, particularly some *Melaleuca* species such as *M. leucadendra*, *M. cajutupi*, *M. viridiflora* are specifically characteristics of freshwater swamps and wetlands in northern Australia (Cowie *et al.* 2000). The grasses and sedges are also typically found in the floodplains in these regions (Cowie *et al.* 2000). While these specific vegetation types are important indicators for suitable nesting sites, they also effectively indicate the presence of freshwater swamps, wetlands, and floodplains for general inhabitation of crocodiles. The availability of these vegetation types also provides hydrological information such as long- or short-term water retention in the areas to support these vegetations (Cowie *et al.* 2000). Hence, the vegetation communities of the *Melaleuca* species, and the grasses and sedges seem an integrated measure of suitable habitat for both living and breeding of crocodiles. I used the ratio of the total area of the favourable vegetation communities to the total area of a catchment as an appropriate measure.

3. Elevation

While the vegetation community variable indicates the available amount of freshwater swamps, wetlands, and floodplains in a catchment as suitable habitat, the model does not incorporate other aspects of the waterbodies such as associated rivers along which these wetlands spread. The suitability of these rivers as habitat seems dependent on their flow or turbulence since crocodiles tend to avoid rapid and turbulent water bodies and stable water current seems a characteristic of their habitat (Burbidge 1987, Webb 1991). Variation in elevation of a catchment may provide a useful surrogate for prevailing water flow regimes. An example is much of the Kimberly region in Western Australia where steep, rugged and deeply sandstones forming waterfalls and associated gorges block access up many rivers for crocodiles (Burbidge 1987, McManara 1994).

Elevation may provide extra information on climate, especially temperature and precipitation. In general, elevated areas in the coastal northern Australia such as Wet Tropics regions in Queensland have lower temperature and higher precipitation than other low regions of the northern Australia (Bureau of Meteorology 2004).

While a number of different variables were possible, elevation range (maximum elevation – minimum) was considered an appropriate measure as each catchment has a portion of its area at sea level.

4. Precipitation

The distribution of *C. porosus* in the tropical regions is typically dominated by a monsoonal climate characterized by two distinct seasons of ‘wet’ and ‘dry’ (Webb 1991, Webb and Manolis 1993b). The cycle of ‘wetting’ and ‘drying’ potentially provides high productivity in the habitat. The high tropical rainfall transports nutrients such as nitrogen and phosphorous to rivers and the tropical water retain large nutrient load deposited in the sediments (Australian Natural Resource Atlas 2004). Many wetland and floodplains associated to those rivers are seasonal with much less water in the dry season, and exposure of the sediments release nutrients that become available to drive another cycle of growth for organisms in the next wet season (PWSNT 2000). Thus, these seasonal waterbodies have potential for very high productivity that supports various fauna and flora. This is in turn likely to support crocodile populations by providing sufficient prey.

In addition, closely related to temperature, the seasonal rains seem to determine the timing and extent of nesting of crocodiles by changing water level; increase in water level in the late dry season to the early wet season stimulates reproductive activities, and decreases in the late wet season likely limit the extent of nesting (Webb 1991, Cooper-Preston and Jenkins 1993).

Thus, a parameter that measures the seasonal patterns of precipitation was considered appropriate to recognize suitable habitat with swamps, wetlands, and floodplains with high productivities in the monsoonal regions. As result, the ratio of total precipitation in one season (wet) to total precipitation in the other season (dry) was considered

appropriate. Direct measurement of the amount of precipitation was not used because it is already partially included in the elevation variable and also no particular study supports the notion of a relationship between the precipitation amount and crocodile abundance.

5. *Saline wetland*

Webb and Manolis (1988; 1993b) speculated that about half of the total population of *C. porosus* in the Northern Territory are distributed in freshwater waterbodies such as freshwater swamps and wetlands while the rest live in tidal rivers with brackish water lined by mangroves. Except for some dominant large individuals in freshwaters, the movement between the marine and freshwater habitats is thought common (Webb and Manolis 1993b, PWSNT 2004).

Mangroves support diverse fauna including insects, fish, crustaceans, birds, reptiles and mammals (Hutchings and Saenger 1987), and their high productivities may contribute to high crocodile abundance. Other waterbodies associated with tidal water such as coastal saline floodplains also provide favourable feeding sites for crocodiles (Webb and Manolis 1993b, Crerar 1997).

As these marine waterbodies are likely to be important components in their habitat, mangroves and saline coastal floodplains were combined as a new variable of saline wetland. The ratio of the total area of the saline wetland to the total area of a catchment or subcatchment is used for this variable.

6. *Landuse type*

It has been consistently claimed that certain types of landuse are influencing the distribution and abundance of *C. porosus* in northern Australia. Taplin (1987; 1990) originally speculated that low densities of crocodiles in Queensland might be resulting from human activities such as cropping, grazing and forestry. Kofron and Smith (2001) surveyed populations in tidal rivers of the populated east coast of north Queensland and suggested that populations still at low densities are suppressed in part by the landuses of urban and rural residential and agricultural development. The

marginal increase of the populations was also observed in historical population analysis from 1994 to 2000 (Read *et al. in press*). They also speculated that habitat degradation and modification due to these landuses was partially responsible for the limited recovery of *C. porosus* in Queensland. Mawson (*in press*) also speculated that degradation of riparian vegetation due to cattle grazing is one of the major environmental factors suppressing crocodile population in Western Australia. However, there has been no study to examine the influences of the landuses on population abundances.

Certain landuses types that are considered most likely to strongly influence the quality of *C. porosus* habitats across northern Australia are used as a human-impact variable. To define landuse types to be included in this variable as 'high-impact', the following criteria were set considering their effects on crocodiles. The high-impact landuses are those that are likely to; 1) change water availability through their direct influence on wetlands or by compromising the hydrological features of catchment, 2) reduce the productivity of catchments that in turn reduces prey availability, and 3) reduce the area of suitable habitat for crocodiles and their prey even if the quality of the remaining habitat remains acceptable. Among the landuse types available in the dataset, the most relevant classes according to these criteria were selected as high-impact landuses (Table 4.5). This variable is presented as the ratio of total area of the 'high impact' landuse to total area of catchment or subcatchment.

Table 4.5. The selected landuse types to be combined as high-impact landuse. The descriptions of the landuses were derived from 'Land Use Mapping at Catchment Scale: Principles, Procedures, and Definitions' (Bureau of Rural Sciences 2002).

Landuse type	Description
Irrigated perennial horticulture	Irrigated crop plants living for more than two years that are intensively cultivated, usually involving a relatively high degree of nutrient, weed and moisture control.
Irrigated seasonal horticulture	Irrigated crop plants living for less than two years that are intensively cultivated, usually involving a relatively high degree of nutrient, weed and moisture control.
Irrigated modified pastures	Irrigated pasture production, both annual and perennial, based on a significant degree of modification or replacement of the initial native vegetation.
Irrigated cropping	Land under irrigated cropping. This class may include land in a rotation system that at other times may be under pasture.
Cropping	Land under cropping. This class may include land in a rotation system that at other times may be under pasture.
Perennial horticulture	Crop plants living for more than two years that are intensively cultivated, usually involving a relatively high degree of nutrient, weed and moisture control.
Seasonal horticulture	Crop plants living for less than two years that are intensively cultivated, usually involving a relatively high degree of nutrient, weed and moisture control.
Plantation forestry	Land on which plantations of trees or shrubs (native or exotic species) has been established for production or environmental and resource protection purposes.
Transport and communication	This class includes airports/aerodromes, roads, railways, ports/water transports, and rader stations.
Residential	This class includes urban and rural residential (houses, hotels, flats, etc).

7. Human population

Human population has also been suggested as an indicator for negative effect on crocodile distribution and abundance, particularly in the east coastal regions of Queensland (Taplin 1987; 1990, Kofron and Smith 2001). Concentration of human population may contribute to a range of factors that suppress crocodile density. Rural and urban residential development is one of the most apparent effects of human population concentration (Taplin 1987, Kofron and Smith 2001). Other adverse activities associated with high human population are possible. Kofron and Smith (2001) suggested that motor boating in the waterways of the populated east coast of Queensland appeared to be one of the human activities keeping the crocodile populations low. Removal of crocodiles for public safety is a more striking factor resulting from human development. In some populated areas, the presence of crocodiles is not tolerated and any crocodiles found in those areas are removed for

public safety. For example, crocodiles are regularly trapped and removed from the Darwin Harbour of the Northern Territory to licensed farms for public safety (PWSNT 2004). Crocodile removal for public safety has been suggested to be responsible for reducing abundances of large animals and to result in limited breeding in Queensland (Kofron and Smith 2001, Read *et al. in press*). Human population density is therefore used as another human-impact variable.

There were a few more factors of interest that could not be used due to limited data availability, although they were suggested as potentially important or relevant in the crocodile literature (Messel and Vorlicek 1987, Webb *et al.* 1998 for water salinity in tidal habitat, Kofron and Smith 2001 for crocodile removal for public safety, and Webb and Manolis 1993b for habitat degradation by feral animals). However, it was considered that there would have minimal loss of ecological information, because the water salinity in tidal habitat, and crocodile removal for public safety are partially included in the variables of saline wetland, and human population density, respectively. The impact of feral animals, especially water buffaloes *Bubalus bubalis*, is also unlikely to be significant in recent years due to the intensive control management conducted in the 1980s (PWSNT 2000, *Bureau of Rural Sciences* 2004).

GIS procedures

The seven environmental variables considered most important in the literature, and catchments and subcatchments were derived from the datasets described above, using a GIS. The GIS datasets used for the variables ranged from 1996 to 2003. This was considered compatible with the crocodile population data ranging from 1997 to 2003 (Tables 4.1 and 4.3). The description of data processing for each variable is provided below.

i. Projection

All GIS data were originally projected in Geographic coordinate system with a datum of either GDA94 (Geocentric Datum of Australia 1994) or WGS84 (World Geodetic System 1984). Each dataset was reprojected into MGA94 (Map Grid of Australia 1994) for vector data or UTM (Universal Transverse Mercator) for raster data. In the

UTM projection, since the study catchments across northern Australia fall into various UTM Zones (Zone 52, 53, 54 and 55), four GIS databases were assembled for this analysis. In the case that a catchment lies over two different zones, it was included in the zone to which more area of the catchment is contained. In addition, the UTM reprojection was modified by 10 000 000 m along the Y-shift (for the southern hemisphere so that the raster data in UTM would be comparative to vector data in MGA94 in corresponding zones).

ii. Catchment and subcatchment

Firstly, the 55 catchments where the crocodile densities are available were extracted from the SWMA dataset into a new layer. The new layer was overlaid with the subcatchment dataset. Referring to the boundaries of corresponding subcatchments, catchments were sub-divided where more than two unconnected rivers with crocodile data existed within the same catchment.

Each catchment and sub-catchment in the sub-divided dataset was then assigned a unique identification value to be characterized with the environmental variables as well as crocodile abundance. The area of each catchment and subcatchment was calculated in km².

iii. Temperature and precipitation

The data for the variables of the mean temperature in the dry season and the ratio of total precipitation in the wet season to total precipitation in the dry season were extracted from ANUCLIM. It requires the input of geocoded data (X, Y and Z values) for calculation at a specified point. In this case, a midpoint in each catchment or sub-catchment was manually selected. The midpoint was assumed to represent the climate of a whole catchment or sub-catchment, especially relevant river systems from which crocodile densities were derived. Since shapes of catchments are often irregular and stretched along rivers, a midpoint was considered around the center of a catchment within approximately 150 km from coastlines. At those midpoints, the X and Y coordinates were recorded in decimal degrees, and Z, the elevation in meters was taken from the DEM. From a number of variables and parameters generated by

ESOCLIM and BIOCLIM, the variables required for the models were extracted (Table 4.6).

Table 4.6. Climatic variables extracted from ANUCLIM (version 5.1) and their definitions derived from ANUCLIM User's Guide (CRE 2000). Two variables of the Precipitation of Warmest Quarter and Precipitation of Coldest Quarter were not directly used for the modelling, but used to generate another variable, the ratio of the total precipitation of the warmest quarter to the coldest quarter.

Mean Temperature of Coldest Quarter	The mean temperature of 13 consecutive weeks that are colder than any other set of 13 consecutive weeks.
Precipitation of Warmest Quarter	Total precipitation over the warmest quarter of the year.
Precipitation of Coldest Quarter	Total precipitation over the coldest quarter of the year.

iv. Vegetation

For the vegetation variable, the datasets of VCTS and RVCQ were used since their classification of vegetation communities included dominant species. From these detailed classes, the most relevant vegetation classes to the favourable vegetation types of the *Melaleuca* species in swamps and wetland, and the grasses and sedges in seasonal floodplains were selected. The selected classes from these data sets were then summarized (Table 4.7).

Table 4.7. Summarized vegetation communities that were considered as requirements for *C. porosus* habitat and their descriptions based on those in the user guides of the Survey and Mapping of 2001 Remnant Vegetation Communities and Regional Ecosystems of Queensland provided (Queensland Herbarium 2001) and the Vegetation Communities of the Tropical Savanna (CRC 2004).

Vegetation community	Description
<i>Melaleuca</i> open forest in perennial wetland and swamp	<i>Melaleuca</i> open forests restricted on wetland and swamps regularly flooded by freshwater or rarely saline water in coastal Northern Territory and northern Queensland. Dominant species include <i>M. viridiflora</i> , <i>M. leucadendra</i> , <i>M. quinquenervia</i> , and <i>M. cajutupi</i> . The ground layer is often a variable mixture of grasses and sedges.
Mixed grasses and sedges species in seasonal floodplain	Complex community consisting of variable grass and sedge species occurring on seasonally inundated floodplain by freshwater or rarely saline water. Dominating grasses include <i>Chrysopogon</i> , <i>Xerochloa</i> , <i>Oryza</i> , <i>Imperata</i> , <i>Themeda</i> species. Sedges such as <i>Baloskion</i> , <i>Meiostachyum</i> , <i>Eleocharis</i> species are also common. Emergent trees may include <i>M. viridiflora</i> .

These two classes were then combined as a variable covering vegetation types known to be associated with *C. porosus* presence in northern Australia. The vegetation communities corresponding to these classes were first extracted from the two datasets as these layers contain numerous polygons. The vegetation communities extracted from the different data sources were then merged into a new GIS layer (Figure 4.3). To recognize which catchment or sub-catchment each vegetation polygon belongs, the merged layer was intersected with the catchment and sub-catchment layer such that each vegetation polygon would be assigned the catchment and sub-catchment ID number in its attribute.

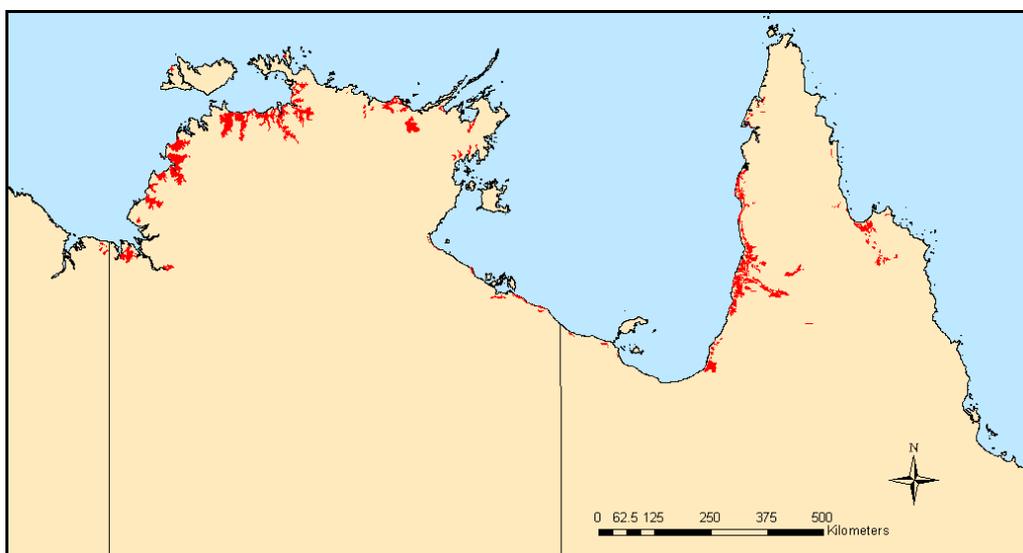


Figure 4.3. Distribution of the *Melaleuca* species in freshwater wetlands, and the grasses and sedges in seasonal floodplains in northern Australia (expressed in red).

The area of each vegetation polygon was calculated in km² and summed on a catchment or sub-catchment basis for each vegetation class. The ratio of the total area of the vegetation community class within a catchment or sub-catchment to the total area of the catchment or sub-catchment was calculated. The ratio was expressed as a percentage to recognize fractional values in the variable.

v. Elevation

Elevation data were derived from the version 2 of the 9-second continental DEM (250m grid cell resolution), which included several tiles that collectively covered northern Australia. These raster tiles were merged to produce a northern Australian

DEM. Basic statistics of the merged elevation raster data were calculated on the catchment or sub-catchment basis. The minimum and maximum elevations were extracted to derive the elevation range in each catchment or sub-catchment.

vi. Saline wetland

For the saline wetland variable (mangroves and saline coastal floodplains), the TOPO 250K dataset was used. Waterbody types that were considered most relevant were extracted into a new layer (Table 4.8). Then, like the vegetation community layer, the new dataset was intersected with the catchment and sub-catchment layer to assign the unique value of the catchment or sub-catchment ID to each vegetation polygon.

After calculating the area of each polygon in km², these individual areas were summarized as the total area of saline wetland in each catchment or sub-catchment. The ratio of the total area of saline wetland within a catchment or sub-catchment to the total area of the catchment or sub-catchment was then calculated as a percentage.

Table 4.8. The selected waterbody types to be combined as saline wetland. Their definitions were those in the GEODATA TOPO 250K Series 2 Product User Guide (Geoscience Australia 2003).

Waterbody type	Definition
Mangrove	A dense growth of mangrove trees, which grow to a uniform height on mud flats in estuarine or salt waters.
Marine swamp	The low-lying part of the backshore areas of tidal waters, usually immediately behind saline coastal flats, which maintains a high salt water content, and is covered with characteristic thick grasses and reed growths.
Saline coastal flat	The nearly level tract of land between mean high water and the line of the highest astronomical tide.

vii. Landuse type

For the data of land use across northern Australia, ‘1996/97 Land Use of Australia, Summary Interpretation for the Australian Natural Resources Atlas (NLWRA), National Land and Water Resources Audit’ was used.

To extract the high-impact landuse types previously defined from the dataset, the layer was reclassified such that the selected landuse types would be assigned the same value to be in one class. Then, basic statistics of the reclassified raster grids, including the total area in km² were calculated on the catchment or sub-catchment basis. The ratio of the total area of the high-impact landuses within a catchment or sub-catchment to the total area of the catchment or sub-catchment was calculated in percentage.

viii. Human population

Cities and major towns where human population concentrates were identified using the GMA 1M dataset. The dataset contains point data of Built-Up Area that is defined as ‘an area containing a concentration of buildings and other structures’ (Geoscience Australia 2004). A total of 25 points were identified in the northern Australia (Table 4.9).

Human demographic data were then attributed to the points of Built-Up Area in northern Australia. The demographic data were derived from the 2001 Census of Population and Housing, Australian Bureau of Statistics.

Based on those demographic data points, a density surface for northern Australia was generated, using a kernel density calculation. Surface density calculation estimates density for a continuous raster surface where data points fall within a circular search area with a specified search distance by summing and dividing specific attribute data of these points by the search area size as each raster cell’s density value (ESRI 2004). In a kernel density calculation, the points lying in cells near the center of the search area are weighted more heavily than those lying near the edge (ESRI 2004). The human density was expressed in persons per km² of catchment or subcatchment.

Table 4.9. Built-Up Area and their populations identified in northern Australia.

Built-up area	Population
Atherton	10621
Ayr	8650
Bowen	8320
Cairns	130000
Charters Towers	8900
Collinsville	2021
Darwin	109419
Derby	9138
Home Hill	3073
Hughenden	2000
Ingham	5500
Innisfail	8500
Kununurra	6100
Mareeba	180960
Mount Isa	26000
Tully	3400
Wulguru	4803

The resulted densities were summarized on catchment and sub-catchment basis. The mean of human density for each catchment or sub-catchment was used to characterize the catchments or sub-catchments.

Candidate models

Having derived the data for the environmental variables, I framed candidate model sets in which each model consists of a specified combination of the variables, based on the biology and ecology of the species, as a hypothesis about the relationship between the population abundance and the environment. The model sets were carefully chosen so that the set would include only the models that are most ecologically relevant, and also the effect of each environmental variable could be recognized. The first set consisted of seven models including natural environmental variables (Table 4.10).

Table 4.10. The first set of candidate models with the natural environmental variables. Notations: y = biomass density of *C. porosus* (kg/km), t = mean temperature in coldest season (°C), v = % of the favourable vegetation community, r = precipitation ratio between warmest and coldest seasons, e = elevation range (m), and s = % of saline wetland.

	Model
1	$y = t$
2	$y = t + v$
3	$y = t + v + r$
4	$y = t + v + r + e$
5	$y = t + v + s$
6	$y = t + v + s + r$
7	$y = t + v + s + r + e$

Model 1 essentially examines the hypothesis that temperature above certain degree is the fundamental requirement of suitable habitat of *C. porosus*, affecting their feeding, movement and breeding.

Model 2 incorporates more localized information for the extent of suitable habitat of crocodiles within catchments and subcatchments. The vegetation variable is expected to identify freshwater wetlands and seasonal floodplains that provide suitable habitat for living and nesting.

In Model 3, it is hypothesized that population density will be higher in highly seasonal rainfall regime because the monsoonal seasonally inundated waterbodies provide high productivity.

Model 4 with the input of the elevation variable assesses the water regimes (flow and turbulence) of the suitable waterbody types and potential climate. It is hypothesized that population will be lower in catchments with high variation in topography.

Model 5 examines in the simplest form a hypothesis that crocodile density will be positively correlated with extent of both freshwater and marine habitats.

Model 6 identifies both freshwater and marine habitat under strong seasonal influences of the monsoonal climate.

Model 7 is a global model, incorporating all of the natural environmental variables that were supported by the literature and for which suitable coverages were available.

As result, the variables of ‘the mean temperature in the coldest quarter of a year’ and ‘the ratio of area of favourable vegetation types in freshwater wetlands and floodplains to the whole catchment area’ were included in all models since they were considered as features of catchments most likely to influence crocodile density.

A second model set was considered to incorporate the human-impact variables in combination with the natural environmental variables (Table 4.11). The combinations were set so that each model would be most ecologically meaningful and the influence of each human-impact model could be examined.

Table 4.11. The second set of candidate models incorporating the human-impact variables. Each model consists of the natural environmental variables of the model selected as best approximating in the first model set, and the human-impact variables. Notations: y = biomass density of *C. prosus* (kg/km), BN = natural environmental variables included in the best-selected model in the first set. h = % of the high-impact landuse types, and p = human population density.

	Model
A	$y = BN + h$
B	$y = BN + p$
C	$y = BN + h + p$

Model A hypothesizes that crocodile density will be lower in a catchment where high-impact landuse occurs in large proportion.

Model B examines the hypothesis that crocodile density will be lower in more dense and settled areas where large human population occurs.

Combining these variables, Model C hypothesizes the additive impacts of landuses that involve substantial change in habitats and the occurrence of high human density.

In addition to the two model sets defined above, the influences of the natural environmental variables and human-impact variables were also compared. The actual goodness of fit of the models was also examined by calculating the changes in deviance of applying the models. It was calculated as proportion of deviance explained by the model in percentage, as follows;

$$D = (ND - RD)/ND$$

Where

D = proportion of deviance explained by the model,

ND = null deviance, and

RD = residual deviance.

Model fitting and selection

These environmental variables and the response variable of the crocodile densities were fitted as Generalized Linear Models (GLM), using R (Version 1.9.1). GLM are an extension of the linear modelling process that allows models to be fitted to data in which variance is not necessarily constant and the errors may not be normally distributed. Crawley (2002) provides practical description of various types of GLM and McCullagh and Nelder (1989) described conceptual issues about the model.

As in many other cases, the response variable of the crocodile density did not follow the normal error structure and it was heavily biased toward low values (Figure 4.4).

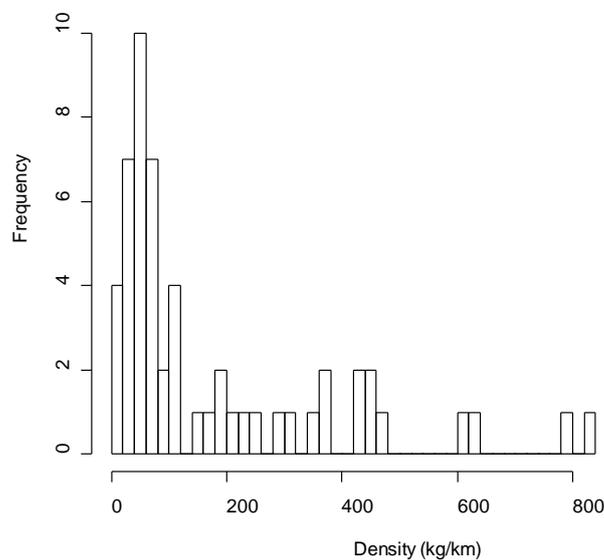


Figure 4.4. Histogram of Crocodile density (kg/km). Note that the response variable values are biased toward zero.

In these cases, Crawley (2002) suggests log-transformation of the response variable and assuming lognormal errors so that the normal error structure and the identity link function can be applied. When log-transformed, the variable showed more normal

distribution than the original data (Figure 4.5). Consequently, the identity link function and normal errors were used for the models.

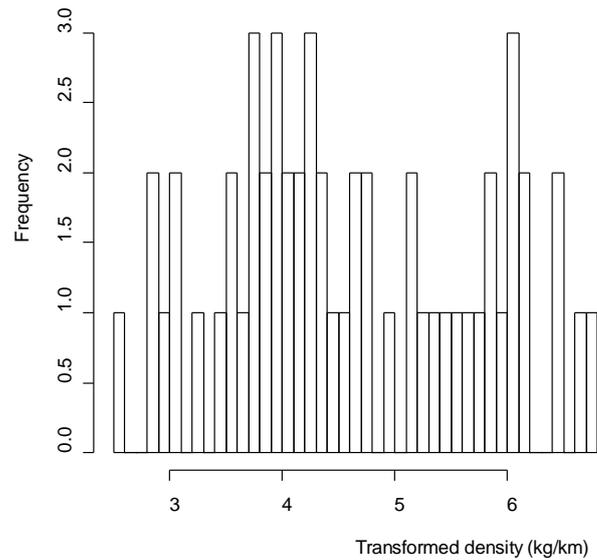


Figure 4.5. Histogram of the log-transformed crocodile density (kg/km). The transformed response variable more closely approximates a normal distribution.

The response variable was also plotted against each explanatory variable. Since all the explanatory variables showed roughly linear relationship with the response variable, they were fitted in linear regression form in the GLM.

After fitting the GLM to the data, model selection statistical parameters were calculated for each model set, following information-theoretic procedures. Since the sample size (n) relative to the number of variables (K) is small (for Model 7, $n/K = 11$), Akaike Information Criterion (corrected) (AICc) was considered an appropriate parameter for the model selection. Accordingly, the differences in AICc between a model with the smallest value and other models (Δ_i) were calculated. The normalized likelihood of model, the Akaike Weight (w_i) was also calculated for each model. Description of each parameter as information theoretic criterion is provided in Chapter 3. The fit of the models was compared in each model set, based on these parameters.

Results

Environmental correlates of crocodile abundance

In the first set of models with the natural environmental variables, all the models except for Model 1 had relatively small variation in the model selection parameters (AICc, Δ_i , and w_i) under the information-theoretic procedures (Table 4.11). While Model 3 had the smallest AICc, Model 1 had the highest value. According to the general rules of Burnham and Anderson (1998; 2001; 2002), Model 2 and Model 6 had ‘substantial support’ since their Δ_i are less than 2 (1.39 and 1.00, respectively). Model 4 showed relatively small values for Δ_i . Model 5 and Model 7 seemed to have much less support as their Δ_i are close to 4 (‘considerably less support’ if $4 \leq \Delta_i \leq 7$ (Burnham and Anderson 1998; 2001; 2002)). With the large Δ_i (18.97), there is likely ‘essentially no support’ for Model 1. These assessments are further reflected in their ‘weight of evidence’ or w_i , which may be interpreted as an approximation of the probability that a model is the actual K-L best model in the set (Burnham and Anderson 2001).

Table 4.12. Model selection statistics for the first set of models with the natural environmental variables. Notations; $\log_e(L)$ = maximized log-likelihood, K = number of parameters, AICc = Akaike information criterion corrected, Δ_i = difference in AICc, w_i = Akaike weight.

Model	$-\log_e(L)$	K	AICc	Δ_i	w_i
1: $y = t$	72.35	3	148.92	18.97	0.00
2: $y = t + v$	62.43	4	131.34	1.39	0.18
3: $y = t + v + r$	60.58	5	129.95	0.00	0.36
4: $y = t + v + r + e$	60.57	6	132.36	2.41	0.11
5: $y = t + v + s$	62.31	5	133.41	3.46	0.06
6: $y = t + v + s + r$	59.86	6	130.95	1.00	0.22
7: $y = t + v + s + r + e$	59.85	7	133.46	3.50	0.06

All of the explanatory variables in Model 3 showed positive relationships with the response variable as expected by the related hypothesis (Table 4.12). The standard errors for the variables were relatively small while that of the intercept was very large compared to the estimate.

Table 4.13. Estimates of variables and their standard errors (*SE*) of Model 3. Notations; *t* = the mean temperature in the coldest quarter of a year, *v* = the ratio of total area of the favourable vegetation types in freshwater wetlands and floodplains, and *r* = the ratio of total precipitation in the coldest quarter to total precipitation in the warmest quarter of a year.

	<i>Estimate</i>	<i>SE</i>
Intercept	0.08	1.32
<i>t</i>	0.18	0.06
<i>v</i>	0.09	0.02
<i>r</i>	0.07	0.04

Models including indices of potential human impact

Since Model 3 had the most support in the first set, an additional set of models dealing with the human-impact variables all incorporated Model 3, as Model A, B, and C. Model selection details are provided in Table 4.13. Model B had a slightly smaller AICc than that of Model A. While the Model C had the largest AICc, the variation (Δ_i of Model C) was small.

Table 4.14. Model selection statistics for the second set of models incorporating the human-impact variables. Notations; $\log_e(L)$ = maximized log-likelihood, *K* = number of parameters, AICc = Akaike information criterion corrected, Δ_i = difference in AICc, *w_i* = Akaike weight.

Model	$-\log_e(L)$	<i>K</i>	AICc	Δ_i	<i>w_i</i>
A: $y = t + v + r + h$	60.56	4	132.34	0.12	0.42
B: $y = t + v + r + p$	60.50	4	132.22	0.00	0.45
C: $y = t + v + r + h + p$	60.48	5	134.72	2.50	0.13

The human population variable had negative effect in Model B as expected by the hypothesis (Table 4.14). However, the standard error of the variable was larger than the estimate.

Table 4.15. Estimates of variables and their standard errors (*SE*) of Model B. Notations; *t* = the mean temperature in the coldest quarter of a year, *v* = the ratio of total area of the favourable vegetation types in freshwater wetlands and floodplains, *r* = the ratio of total precipitation in the coldest quarter to total precipitation in the warmest quarter of a year, and *p* = human population density per km³ of catchment.

	<i>Estimate</i>	<i>SE</i>
Intercept	0.66	2.02
<i>t</i>	0.16	0.09
<i>v</i>	0.09	0.02
<i>r</i>	0.07	0.04
<i>p</i>	-0.05	0.13

The comparison between the best-selected models from the first and second sets showed that the best natural environmental model had smaller AICc than the best

human-impact model although the difference was not significant ($\Delta_i = 2.27$) (Table 4.15). The weight of the natural environmental model was consequently higher than the human-impact model. The proportion of deviances explained by each model was reasonably high while that of the best human-impact model was slightly higher than the best natural environmental model.

Table 4.16. Model selection statistics for the comparison between a natural environmental model (Model 3) and a model incorporating the human-impact variable (Model B) from the two sets defined above. Notations; $\log_e(L)$ = maximized log-likelihood, K = number of parameters, AICc = Akaike information criterion corrected, Δ_i = difference in AICc, w_i = Akaike weight, and D = percentage of deviance explained by the models.

Model	$-\log_e(L)$	K	AICc	Δ_i	w_i	D
3: $y = t + v + r$	60.58	3	129.95	0.00	0.76	56.89
B: $y = t + v + r + p$	60.50	4	132.22	2.27	0.24	57.01

Discussion

One of the strengths of information theoretic procedures is that they provide quantitative evidence for each model in a set rather than the dichotomy of the null hypothesis test (Anderson and Burnham 2002). This allows flexible evaluation and interpretation of the quantitative evidence regarding biological or ecological hypotheses.

Although the differences between the models are not definitive, the model selection statistics most strongly supported a model based on the variables of the mean temperature in the coldest quarter of a year, the ratio of total area of the favourable vegetation communities in freshwater wetland and floodplain to catchment or subcatchment area, and the ratio of total precipitation in the warmest quarter to the coldest quarter of a year. The model suggests that they are important variables to describe the crocodile abundance data.

Moreover, the models that had essentially equivalent support (Model 2, 3, and 5) consistently included the variables of the mean temperature in the coldest quarter of a year, and the ratio of total area of the favourable vegetation communities in freshwater wetland and floodplain to catchment or subcatchment area.

The relative importance of the variables in the best model is highlighted when taking account of their effect sizes on crocodile abundance (Figures 4.6 and 4.7). Figure 4.6 shows that the variable of the favourable vegetation communities in freshwater wetland and floodplain to catchment or subcatchment area has more effect on the predicted densities of crocodiles than the variables of the mean temperature in the coldest quarter in year.

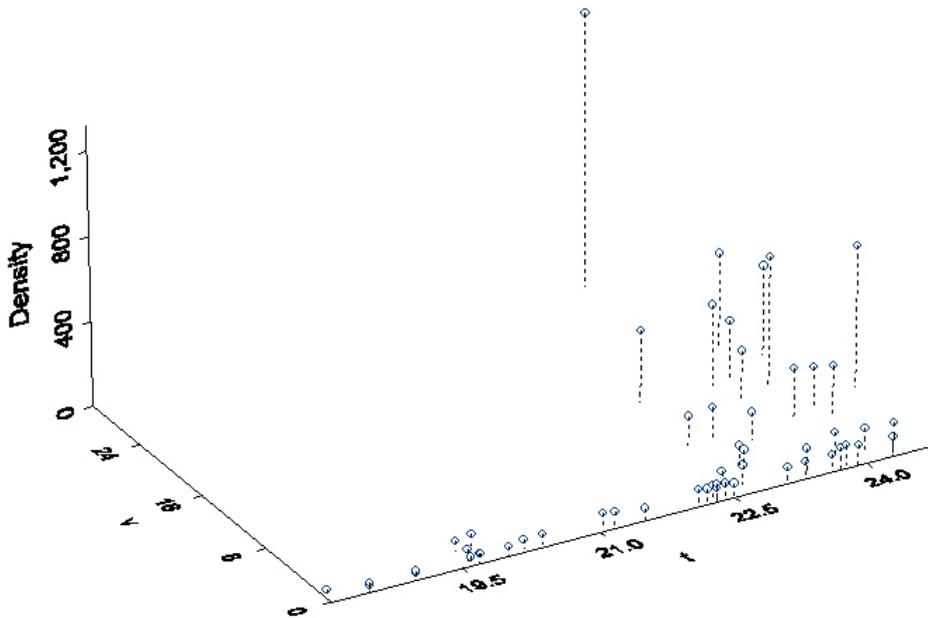


Figure 4.6. 3D plot of predicted crocodile density and the variables of the mean temperature in the coldest quarter in a year (t), and the ratio of suitable vegetation in wetland and floodplain (v).

On the other hand, the variables of the mean temperature in the coldest quarter in year, and the ratio of total precipitation in the warmest quarter to the coldest quarter of a year seem to have relatively similar effects on the predicted crocodile densities (Figure 4.7).

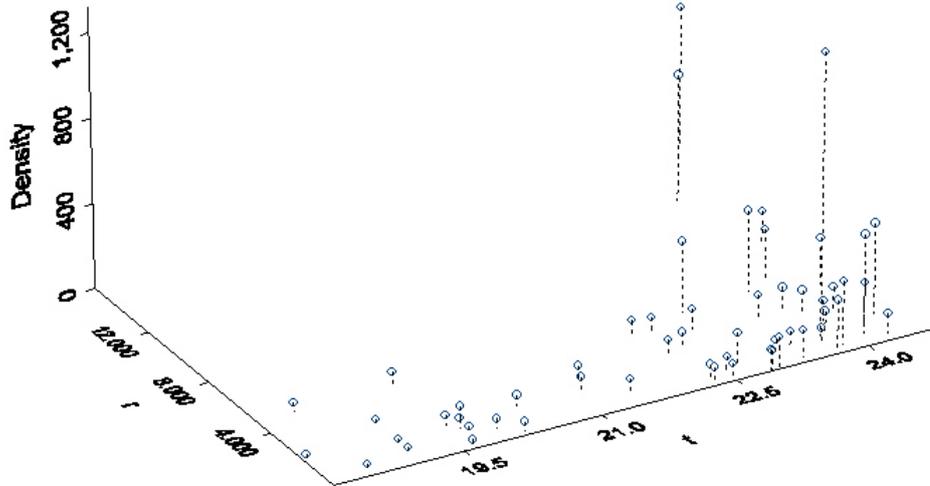


Figure 4.7. 3D plot of predicted crocodile density and the variables of the mean temperature in the coldest quarter of a year (t), and the ratio of total precipitation in the warmest quarter in a year to that of the coldest quarter in a year (r).

The particular effect of the favourable vegetation communities in freshwater wetland and floodplain to catchment or subcatchment area supports the hypothesis that the *Melaleuca* species in freshwater wetlands and, grasses and sedges in seasonal floodplains provides the high quality of habitat in term of breeding and feeding. Catchments or subcatchments that had the highest ratio of the favourable vegetation were the Reynolds, Wildman, and West Alligator Rivers in the Northern Territory while many in Queensland and all in Western Australia (the Ord River and West Arm) had no representation of this variable type.

The variable of the mean temperature in the coldest quarter in year also has some effect, suggesting that the temperature above certain degree is important requirement for their feeding, movement and breeding

The ratio of total precipitation in the warmest quarter to that in the coldest quarter of a year is likely to have effectively recognized the monsoonal regions. The model showed some evidence for the hypothesis that the highly seasonal rainfall in the monsoonal climate is important for the species, providing high productivity to their habitat.

While these variables were selected as the model best describing the crocodile abundance data, my treatment does not prove that other variables are unimportant.

Given that the difference in the level of support for other models including elevation range, and saline wetland was relatively small, we can draw no strong conclusion about the contribution of these features to support of *C. porosus* populations.

If the goal is prediction of the dependent or response variable (eg. crocodile density), Burnham and Anderson (1998; 2001; 2002) suggest multi-model inference (MMI) in which the inference is based on the entire set of models rather than one selected model. MMI reduces model selection uncertainty in making prediction, using all models in the *a priori* set weighted by their respective Akaike weights (w_i).

The entire set of models can also be used for assessing the relative importance of predictor or explanatory variables (Burnham and Anderson 1998; 2001). The predictor's importance may be determined by summing w_i for each variable across all models that include the variable in a set. This requires 'design' considerations about hypothesis (model) building (Burnham and Anderson 2001) – balance of models with or without variables such that variables appear in models at equal or close frequency. In this analysis, however, the models were constructed based on the ecological meaning for the species rather than balancing the distribution of each variable in the set. As result, all the models had the temperature and vegetation variables in common because these variables summarise fundamental requirements of the species. It was considered inappropriate to balance the models by excluding these fundamental variables from some models at potential expense of being 'unrealistic' in ecological sense.

Over all, the *a priori* models based on the species ecology and biology suggest that the variables of temperature, vegetation and precipitation have reasonable level of support. Their various effect sizes (Figures 4.6 and 4.7) also suggest that the vegetation variable has the most influence while the temperature and precipitation variables have similar level of effect.

Given that these variables provide the best model of the natural environmental influence, the model including human population had the most support in the second model set, although the other variable of high-impact landuse also had very similar level of support (Table 4.13).

More importantly, when comparing the model including the human population variable to the best natural environment model, the natural environmental variables appear more likely to be influencing the crocodile abundance than the human-impact variable (Table 4.16). In addition, I examined an extra set of models that consisted exclusively of human-impact variables and the models consistently showed very high AIC_c values, suggesting virtually no support for those models.

The best models also showed relatively high proportion of deviance explained (Table 4. 16), suggesting that they can reasonably be useful in terms of predictive power as ecological models.

Taken together, the model selection based on the theoretic information approach shows that variation in the abundance of *C. porosus* in northern Australia can be clearly related to natural environmental variation. At the broad scale and resolution of this analysis, there was no clear evidence of a relation with levels of agricultural modification of the landscape nor human population density. This is not to say that there is no such relationship, but that the data available provided little support for this hypothesis. Improvements in the quality of data or changes in the scale of analysis may produce different results.

While the models suggest external influences from specific aspects of the environment, there may also be ‘intrinsic’ factors that limit populations. In many cases, wildlife populations are density-dependent, where the size of population is internally regulated by intraspecific competition for resources (Bailey 1984, Caughley and Sinclair 1994, Stiling 2002). One of the common intraspecific competitions is ‘interference competition’ that involves direct interaction of individuals through their behaviour (Caughley and Sinclair 1994). *C. porosus* may be a good example for this type of competition, considering that the species often shows behavioural interference with some dominant individuals excluding subordinate ones from their territories, or favourable places (Cooper-Preston and Jenkins 1993, Webb and Manolis 1988, Webb and Manolis 1993b). In their thermoregulatory behaviour, large individuals tend to dominate riverbanks for basking or access to water to avoid excessive heat (Lang 1987a, Webb and Manolis 1993b). Females of *C. porosus* are also known to compete

for favourable nesting sites and some dominant individuals are intolerant of others nesting close to them (Webb and Manolis 1993b). The most direct behavioural interference is cannibalism with larger individuals feeding on smaller ones (Webb and Manolis 1988). Webb and Manolis (1993b) suggested that the cannibalistic behaviour is effectively controlling population size. It is likely that *C. porosus* populations are to some extent influenced by such internal regulating factors.

However, the previous analysis in Chapter 3 has showed that the contemporary populations are apparently approaching different levels of asymptote in different major river systems, suggesting that the quality of the environment is imposing a strong influence, rather than there being a particular density determined by intraspecific behavioural interference. Moreover, populations at much higher densities are found in captivity (pers. observation). When maintained at very high densities in captivity, *C. porosus* shows partial adaptation to crowded conditions with minor behavioural interference (Webb and Manolis 1988, Webb and Manolis 1993b). This indicates their ability to tolerate higher densities than presently observed in even the best natural habitats. If there is an 'intrinsic' maximum density to which wild populations are limited, it would appear to be much higher than the densities of any contemporary wild populations.

In conclusion, the contemporary populations of *C. porosus* in northern Australia seem to be primarily affected by the quality of environments available to them. Although there have undoubtedly been major environmental changes in parts of their range in Australia, I was unable to clearly relate these changes to variation in density, at the very broad (catchment level) scale. It would be useful to repeat these analyses with other indices of landuse change and at a finer scale.

This inference based on model selection raises a number of implications for management of the species, which are discussed in the next chapter.

CHAPTER 5

Management Implications

5.1. Climate change

The hypothesis-based models showed that the population abundance of *C. porosus* across Australia is likely most strongly influenced by broad environmental variables. These variables are 1) the mean temperature in the coldest quarter of a year, 2) the ratio of total area of *Melaleuca* species in freshwater swamps and wetlands and grasses and sedges in seasonal floodplains to catchment area, and 3) the ratio of total precipitation in the warmest quarter of a year to that in the coldest quarter of a year.

The modelled relationship between the species and environmental factors has important implications for the species distribution and abundance.

There have been apparent changes in climate, known as ‘global warming’, largely caused by human activities increasing greenhouse gas concentration in the atmosphere (CSIRO 2001a; 2001b, Hughes 2003). The effect of global warming has been observed and predicted to affect on various aspects of the environment in Australia (CSIRO 2001a, Hughes 2003).

The temperature has increased up to 0.8 °C over the last century in Australia and historical records show that the minimum temperature has risen more rapidly than the maximum (Hughes 2003). If the minimum temperatures consistently increase across northern Australia, it may indicate a potential positive effect on crocodile abundance by enlarging the range of distribution. This would extend crocodile distribution and increase relative abundance in the sub-tropical parts of Australia that support denser human populations with no previous experience of crocodiles. The potential for adverse interaction is likely to increase.

Precipitation has also altered. It has been estimated that annual total precipitation in the Northern Territory increased by approximately 15% over the last century. More importantly, precipitation has increased more in summer than winter on the continent

basis (Hughes 2003). This might have increased rainfall seasonality between the wet and dry season in northern Australia as another positive effect on the species.

On the other hand, it has been observed that extensive seasonal freshwater swamps and floodplains in northern Australia are being affected by saltwater intrusion (Whitehead *et al.* 1990, PWSNT 2000, Hughes 2003). In the Mary River of Northern Territory, tidal creek systems have been expanding into freshwater wetlands at the rate of 0.5 km per year (Hughes 2003). The saltwater intrusion has already destroyed hundreds of km³ of *Melaleuca* open forest in the freshwater wetland system of the river (PWSNT 2000). This is likely to have significant effect on the species by limiting the availability of suitable nesting site and prey. Barriers have been progressively constructed to prevent the saltwater intrusion in the river (PWSNT 2000). Saltwater intrusion also enhances the expansion of mangrove communities (Eliot *et al.* 1999, Hughes 2003), and as the species is distributed in both types of waterbodies as major habitat, it is difficult to predict the net effect on them. However, my broad scale models suggest that negative effects are more likely than positive, especially in the Northern Territory where major wetlands and floodplains at or near existing sea levels provide much of the best *C. porosus* habitat.

5.2. Management of wetland and floodplain

As the climatic variables are not under local control, management to promote continued availability of the favourable vegetation communities in the freshwater wetlands, swamps, and floodplains seems of primary importance for the species management. These vegetation communities and waterbodies are likely to be affected by a range of human activities. PWSNT (2000) summarizes potential threats to extensive wetland systems in the Northern Territory. As these are likely to be relevant to Queensland and Western Australia, each threatening factor is briefly described below in relation to *C. porosus*.

Feral animals such as water buffalo *Bubalus bubalis* are known to adversely affect wetlands and floodplains (Skeat *et al.* 1996). While many waterbodies have significantly recovered since the control programs in the 1980s in the Northern Territory, populations are recovering in parts of Arnhem Land (PWSNT 2000). Exotic

plants such as *Mimosa pigra* may also have negative impacts on *C. porosus* by replacing riparian native plants, reducing access to suitable vegetation for nesting and prey that feed on the native plants (Braithwaite *et al.* 1989, Cowei *et al.* 2000).

Pasturing for livestock grazing is one of the sources of exotic plants (Cowe *et al.* 2000). Monoculture of introduced grass can replace diverse native plants in wetlands, the reducing productivity of the waterbodies. Intensive grazing also reduces the density of vegetation that provides suitable nesting sites and prey.

The productivity of wetland and floodplain may also be reduced by pollution (Cosser 1997). Water pollution can be caused by mining by-products, urban run-off, biocides from agriculture, and waste disposal (PWSNT 2000). Water pollution may directly or indirectly affect the species. However, there is no evidence that such pollution is having any effects on contemporary crocodile populations.

Tourism and recreation may also disturb diverse biota in wetland and floodplain habitat (PWSNT 2000). It has another particular effect on crocodiles, imposing call for removal or culling for public safety as explored in the previous analysis. On the other hand, as an iconic wildlife in Top End, the species attracts large number of tourists, which provides one of the most important incentives for the conservation and management of the environment and the species (Webb and Manolis 1993a; PWSNT 2004).

In short, all the natural environmental variables that I have shown likely to influence the abundance of *C. porosus* in northern Australia may be affected by global warming: namely increasing temperature, precipitation, and sea level. While the variables of temperature and precipitation may not immediately be affected by human activities, the variable of the favourable vegetation communities in suitable freshwater habitat is more directly affected by human impacts. Of particular concern will be forms of use that divert water from floodplain systems and rivers to agricultural or urban use (Schofield *et al.* 2003). The quality of management of freshwater wetlands and seasonal floodplains and the water that sustains them is likely to be the single most important determinant of the status of this iconic species.

CHAPTER 6

Conclusions

6.1. Population recovery of *C. porosus*

The comparison of population abundance estimates of *C. porosus* between the contemporary and pre-hunting period in the Northern Territory showed that the various contemporary density estimates match reasonably with the pre-hunting density estimates, suggesting that the recovery of the contemporary populations from hunting has advanced to levels now comparable to those before the hunting.

Trends in population growth of the individual rivers over the period since protection were determined by fitting population growth models. The information theoretic criteria showed strong evidence for the logistic model rather than the linear and exponential models. The predicted asymptotes of the logistic models were close to the contemporary densities observed in these rivers, further suggesting that the recovery of *C. porosus* populations is well advanced in most river systems of the Northern Territory and the rate of population increase is now being limited by the quality of the environment rather than the impact from the past hunting.

Assuming the highest intrinsic rate of increase of the Mary River as the maximum rate of increase of *C. porosus* in northern Australia, the maximum rate of increase of *C. porosus* was higher than that of other poikilotherms. Their high fecundity and optimum environment conditions may explain their rapid recovery in the Northern Territory.

6.2. Species-environment relationship

A process of model selection from a set of the hypothesis-driven models about relationships between population abundance and the environment – based on the species' biology and ecology – showed strong support for a model with natural environmental variables of 1) 'the mean temperature in the coldest quarter of a year', 2) 'the ratio of total area of freshwater wetland dominated by the *Melaleuca* species

and seasonal floodplain dominated by the grass and sedge to total area of catchment or subcatchment’, and 3) ‘the ratio of total precipitation in the warmest quarter of a year to total precipitation in the coldest quarter of a year’.

The results also showed little support for models incorporating human-impact variables, suggesting that contemporary population abundance of the species appears to be primarily influenced by the quality of the natural environment rather than the contemporary impact of human activities. However, further examination of these questions using different datasets at finer scales may produce different results. Subsetting northern Australian regions as new study area, finer-scaled GIS datasets that contain more regional characteristics in the environment should detect the crocodile abundance-environment relationship that the broad scale of this study might not be able to find. Such additional work should be accorded a high priority, if concerns about the rate of recovery in Queensland in particular are to be seriously addressed.

Intrinsic regulation through behavioural interference is unlikely to be the major influence limiting wild populations. If there is an ‘intrinsic’ maximum density for the species in the wild, it would appear to be much higher than the densities of any contemporary wild populations, including such highly favourable sites as the Mary River in the Northern Territory, or populations existing prior to commercial hunting.

6.3. Management implication

The natural environmental factors selected as best describing the variation in population abundance of *C. porosus* in northern Australia are all likely affected by the global warming including the increase in temperature, precipitation, and sea level due to global warming. Maintaining the favourable vegetation communities in freshwater wetlands and seasonal floodplains appears the primary management issue for maintaining the species abundance in northern Australia. There are many incentives to actively protect these habitats, including the significance of *C. porosus* to the region's Indigenous people, its status as a symbol of the Northern Territory's healthy wetland systems, and its economic value as a mainstay of the tourism industry.

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