THE SEX AND SURVIVORSHIP OF EMBRYOS AND HATCHLINGS

OF THE AUSTRALIAN FRESHWATER CROCODILE,

CROCODYLUS JOHNSTONI

A thesis submitted for the degree of

Doctor of Philosophy

of the Australian National University

by

Anthony Michael Arthur Smith

August 1987
Declaration

I declare that this thesis is all my own work, except where duly acknowledged, and has not been presented for the award of any other degree or diploma in any University.

Anthony M.A. Smith
Acknowledgements

This study would not have been possible without the help of many people. Particular assistance in field work was provided by Karen Dempsey, Peter Whitehead, David Choquenot, Anita Gordon, Jane Ambrose, Don Garling, Kerry Richens, Rod Kennett, Rik Buckworth, Jenny Buckworth, Tim Wood, Bridget Bonnin, Allan Heckenberg, Ann Rich, Mark Dickens, Ian Trapnell, Tony Spring, Raoul Mulder, Harvey Cooper-Preston, Neville Haskins, and the late Chip Rogers. Additional assistance and advice came from Charlie Manolis, Jenny Powers, and Bill Freeland.

Ross Cunningham provided extensive advice on a variety of statistical techniques. However, any errors in the implementation or interpretation of statistics are my own. David Sandilands and David Smith were most helpful with computer implementation of statistical and other software. Gary Brown produced most of the figures in this thesis. Appendix 1 benefitted from comments by Ross Cunningham, Jim Bull and Michael Ewert.

My time at RSBS was enriched by numerous interactions with members of staff and fellow students. Of those, I would particularly like to thank Mike Arnold, John Benzie, Peter Christian, Les Christidis, David Coates, Don Colgan, Adam Marchant, David Rowell, and David Shaw.
I am indebted to my supervisors Grahame Webb, Barney John and Max King for advice, guidance, and encouragement throughout the course of this study.

This study was funded by the Research School of Biological Sciences at the Australian National University, with additional support from the Conservation Commission of the Northern Territory, the Northern Territory University Planning Authority, and the North Australia Research Unit of the Australian National University.

Finally, I thank my family for support and encouragement throughout the course of this study.
IV

Abstract

The ecology of nesting of the Australian Freshwater Crocodile, *Crocodylus johnstoni*, was examined over three years in the McKinlay River area, Northern Territory. The study centred on that period of time from the onset of the nesting season, until the hatchlings were up to one month old.

Nest site selection was found to be based on the avoidance of grassed areas, and on the occurrence of an appropriately high substrate temperature. There was an ordering of females during the nesting season such that larger females tended to nest before smaller females. This effect was suggested to be age rather than size dependent. Embryos had their sex determined by the egg incubation environment during that period between 20-50% of incubation. Temperature was identified as the most important environmental correlate of sex, although an influence of substrate type was found and appeared to relate to the hydric and/or gaseous environment of the nest. The day on which a nest was laid was the primary determinant of subsequent temperature. Hatchling sex ratio was, thus, largely dependent on the day on which the clutch was laid. Given the trends between female size and day of laying and between day of laying and sex ratio, a relationship is inferred between the size/age of a female and the sex of her offspring: young and old females tend to produce females whereas middle aged females tend to produce males. Embryo mortality occurred primarily through predation by *Varanus gouldii*. Such mortality appeared to be random. Minor environmental influences on embryo mortality were identified, but accounted for few embryos.
Embryonic sex determination and survival appear unrelated. The size of hatchlings appeared to be largely determined by the size of their egg.

Hatchling survival was examined in two years. Mortality was high (approximately 50%) over the average of about 20 days the animals spent at liberty. Survival was not random and the action of stabilising selection was identified. Head length at hatching was correlated to survival such that animals with particularly large or small heads had a lower probability of survival. Temperatures at particular times during incubation were also correlated with survival. Neither sex had a consistent survival advantage. It was argued that the pattern of hatchling survival reflects the optimality of the nest environment.

The bearing of these data on the evolution and maintenance of environmental sex determination was discussed. It was concluded that this study identified the action of selective forces not previously considered and that such forces need to be accommodated by any hypothesis concerning the evolution and maintenance of environmental sex determination.
CHAPTER 1 INTRODUCTION

1.1 GENERAL

1.2 GENOTYPIC SEX DETERMINATION

1.3 ENVIRONMENTAL SEX DETERMINATION
   1.3.1 General
   1.3.2 Invertebrates
   1.3.3 Vertebrates
      1.3.3.1 Fish
      1.3.3.2 Amphibians
      1.3.3.3 Birds and mammals
   1.3.4 Reptiles
      1.3.4.1 General
      1.3.4.2 Environmental variables
      1.3.4.3 Genetic influences
      1.3.4.4 Available laboratory and field data
   1.3.5 The proposed molecular basis of environmental sex determination
   1.3.6 The proposed theoretical basis of environmental sex determination

1.4 THE SUITABILITY OF CROCODYLUS JOHNSTONI AS AN EXPERIMENTAL ANIMAL

1.5 AIMS OF THIS STUDY
CHAPTER 2 THE MCKINLAY RIVER AREA AND ITS CROCODYLUS JOHNSTONI POPULATION

2.1 GENERAL

2.2 THE MCKINLAY RIVER STUDY AREA

2.2.1 The general study area

2.2.2 Climate

2.2.3 Major study sites

2.2.3.1 Site one

2.2.3.2 Site two

2.2.3.3 Site three

2.2.3.4 Site four

2.2.3.5 Site five

2.2.3.6 Site six

2.2.3.7 Site seven

2.3 THE POPULATION AND ITS DISTRIBUTION

2.3.1 Population size

2.3.2 Dry season distribution

2.3.3 Wet season distribution

2.4 GROWTH, MOVEMENT AND THE POPULATION STRUCTURE

2.4.1 Growth

2.4.2 The population age and sex structure

2.4.3 Survivorship

2.4.4 Movement

2.5 DIET AND FEEDING
2.6 REPRODUCTION

2.6.1 Size and age at maturity
2.6.2 Courtship and mating
2.6.3 Nesting
2.6.4 Embryo ecology
2.6.5 Hatching

2.7 PREVIOUS UTILISATION AND RESEARCH INFLUENCES

2.7.1 Hunting
2.7.2 Research influences

CHAPTER 3 METHODS

3.1 THE LOCATING OF NESTS AND THE MEASUREMENT OF BASIC PARAMETERS
3.2 THE ESTIMATION OF LAYING DATE
3.3 THE RELOCATION OF NESTS
3.4 NEST EXCAVATION AND THE MAPPING OF NESTS
3.5 CLASSIFICATION OF EGGS AND EMBRYOS
3.6 STATISTICAL ANALYSES

CHAPTER 4 NESTING

4.1 INTRODUCTION
4.2 RESULTS

4.2.1 Relationships between female size and clutch parameters
4.2.2 Nest sites and their selection

4.2.2.1 General
4.2.2.2 Methods
4.2.2.3 Results
4.2.3 Time of nesting

4.2.4 Variation in clutch characteristics with respect to day of laying

4.2.5 Variation in total nesting effort and clutch parameters among years

4.2.6 The correlation structure of nesting

4.3 DISCUSSION

4.3.1 The relationship between female size and clutch parameters

4.3.2 Nest sites and their selection

4.3.3 The time of nesting

4.3.4 Variation in clutch parameters with respect to day of laying

4.3.5 Variation in clutch parameters and total nesting effort among years

CHAPTER 5 THE ECOLOGY OF EGGS AND EMBRYOS

5.1 INTRODUCTION

5.2 RESULTS

5.2.1 Primary mortality

5.2.1.1 Incidence of predation by varanids

5.2.1.2 The influence of egg shape on subsequent development

5.2.1.3 The influence of egg angle on subsequent development

5.2.1.4 Incidence of infertility or no apparent development and its relationship to clutch size
5.2.1.5 Influence of egg size on the success of viable eggs 95
5.2.1.6 The relationship between sex and non-survival, and the affect of relocation 95
5.2.1.7 Flooding 96
5.2.2 The thermal environment of Crocodylus johnstoni nests 97
5.2.3 The relationship between sex and nest temperature 103
5.2.4 The relationship between nest temperature and total incubation time 108
5.2.5 The relationship between sex and day of laying 109
5.2.6 The relationship between nest temperature and the incidence of normal hatchlings 110
5.2.7 The determinants of hatchling size 112
5.2.8 Hatching 114
5.3 DISCUSSION 116
5.3.1 Primary egg mortality 116
5.3.1.1 The incidence of predation by varanids 116
5.3.1.2 The influence of egg shape on subsequent development and its relationship to clutch size 118
5.3.1.3 The influence of egg angle and egg size on subsequent development 119
5.3.1.4 The relationship between sex and non-survival, and the affect of relocation 120
5.3.1.5 Flooding 120
5.3.2 The thermal environment of nests, and its relation to the sex and survival of embryos 121
5.3.2.1 The thermal environment of nests 121
5.3.2.2 Nest temperature and the sex of embryos 122
5.3.2.3 The relationship between nest temperature and total incubation time 124
5.3.2.4 The relationship between day of laying and embryonic sex 125
5.3.2.5 The relationship between nest temperature and embryo survivorship 126
5.3.2.6 The determinants of hatchling size 127

5.3.3 Hatching 128

CHAPTER 6 SHORT-TERM SURVIVAL AND GROWTH OF HATCHLINGS 130

6.1 INTRODUCTION 130
6.2 METHODS 132
6.2.1 Number and sources of animals released 132
6.2.2 Recapture of hatchlings 133
6.2.3 Capture and stomach pumping of larger crocodiles 134
6.3 RESULTS 134
6.3.1 Dimensions and characteristics of hatchlings released 134
6.3.2 Relationship between day of release and the physical characteristics of hatchlings 135
6.3.3 Dimensions and characteristics of hatchlings recaptured 136
6.3.4 Evidence for the action of natural selection 138
6.3.5 Analysis of hatchling survival 139
6.3.6 Analysis of hatchling growth 144
6.3.7 Stomach contents of larger crocodiles 146

6.4 DISCUSSION 146
6.4.1 Extent and causes of mortality 146
6.4.2 The action of natural selection 147
6.4.3 Hatchling survival 149
CHAPTER 7 SYNTHESIS AND CONCLUSIONS

7.1 GENERAL

7.2 ANSWERS TO FIVE QUESTIONS

7.3 IS THERE A GENERAL PATTERN TO SEX DETERMINATION AND SURVIVAL IN CROCODILES

7.4 ON THE EVOLUTION AND MAINTENANCE OF ENVIRONMENTAL SEX DETERMINATION

7.5 INDICATIONS FOR FURTHER WORK

LITERATURE CITED

APPENDIX 1 Pivotal, threshold and sex determining temperatures:

Variation in Caretta caretta and Graptemys pseudogeographica.

APPENDIX 2 A method for estimating residual yolk mass in hatchling crocodilians.

APPENDIX 3 Crocodylus johnstoni in the McKinlay River Area, N.T.

VII. A population simulation model.
CHAPTER 1

INTRODUCTION

"Logic is the art of going wrong with confidence.”

(Anon)

1.1 GENERAL

An individual’s sex is typically determined by the precise balance of genetic sex determinants established at fertilisation (Genotypic Sex Determination; GSD). This balance serves as a trigger which switches gonadal differentiation into either a male or female mode. However, in some cases, the trigger which guides the mode of gonadal differentiation appears wholly determined by the environment which the individual experiences early in embryonic development (Environmental Sex Determination; ESD). These two modes, genotypic and environmental sex determination, are not mutually exclusive evolutionary paths. Instead, they may be seen as the end points of a spectrum of genetic and environmental influences on sex. Indeed, in many fish and amphibians which possess GSD, environmental influences are known to be able to override the genotypic sex (Bacci 1965).

Our knowledge of GSD has grown rapidly and extensively since the rediscovery of Mendelian genetics. Although the first observations of ESD were made in invertebrates at around the same time (Baltzer 1912), there has been little substantive progress in defining accurately the extent to which ESD operates in invertebrates.

Despite these numerous studies, our knowledge and understanding of environmental sex determination still remains rudimentary (Bulmer 1987). Crocodiles, however, offer a unique opportunity to examine the mechanism of ESD in some detail. Extensive laboratory studies of ESD in crocodiles have been completed, and the basics of crocodile ecology are now sufficiently well known to allow an examination of the ecological aspects of ESD in natural populations.

Environmental sex determination in crocodiles occurs during embryonic development, which is the most critical of the life history stages (Webb and Smith 1984, 1987; Smith and Webb 1985). Not only is sex determined during this time but generally low and extremely
variable survivorship of embryos has been observed (Webb, Buckworth and Manolis 1983d; Webb, Sack, Buckworth and Manolis 1984; Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987; Hutton 1984, 1987; Ferguson 1985). Furthermore, embryonic sex determination and survival are not independent since both appear to vary in response to the same environmental variables, and the quality of the incubation environment may have lasting effects on the post-hatching animal, perhaps by determining its growth potential (Joanen et al. 1987; Webb, Beal, Manolis and Dempsey 1987). Significantly, Schwarzkopf and Brooks (1985) indicate that the relationship between sex and survival in the turtle *Chrysemys picta* is not the same in field and laboratory situations, as has also been shown for *C. johnstoni* (Webb and Smith 1984). In both these cases, survival in the laboratory exceeds that in the wild by a considerable amount. This is not surprising since conditions in the laboratory are aimed at optimising survival. Thus, not only are sex determination and embryo survival best considered together, but there is a clear need for extensive field studies of ESD to complement the ever-growing body of laboratory data.

1.2 GENOTYPIC SEX DETERMINATION

In some animal groups, especially fish, there exists a continuum of influences on sex determination ranging from predominantly genetic to predominantly environmental (Bacci 1965; Bull 1983). Among reptiles, however, there is no such continuum: species either have their sex determined entirely in response to the environment (ESD), or without regard to it (GSD) (Bull 1980, 1983; Olmo 1986).
There are many forms of GSD, yet they have in common the fact that sex is determined at the time of gametic fusion on the basis of the zygotic genotype (see for example Bacci 1965; Crew 1965; Mittwoch 1973; Austin and Edwards 1981; Bull 1983). All forms of GSD among animals involve systems of either male or female heterogamety. Most usually, these systems are coupled to morphologically distinct sex chromosomes, and here the critical switch genes which govern the precise pattern of sexual differentiation in the neuter gonad are carried on one or other of these chromosomes.

Individual reptile species with GSD exhibit either male or female heterogamety, sometimes, though not always, accompanied by sex chromosome differentiation (Bull 1980; Olmo 1986). Although in some groups there are more than two sex related chromosomes, the basis of sex determination is still dependent on a simple switch mechanism (Bull 1980, 1983). Following the classification of reptiles proposed by Olmo (1986), sex chromosomes have been identified in at least some species of the Chelonia, Sauria and Ophidia where they are considered to be of relatively recent origin. They appear to have evolved independently on a large number of occasions, and in different species either the male or the female may function as the heterogametic sex (Bull 1983; Olmo 1986).
1.3 ENVIRONMENTAL SEX DETERMINATION

1.3.1 GENERAL

Bull's (1983, p8) definition of ESD is sex determined during embryogenesis "in response to the local environment, with some environments producing males and others females"; and where "sex cannot be predicted by zygotic genotype, because of the subsequent environmental influence". This definition, though generally acceptable, is too simplistic, since it fails to account for the true lability of sex determination in many species. For example, in the marine echiurid worm Bonellia viridis, which is a well known case of ESD, not all individuals (10-20%) have their sex determined in response to the environment (Jaccarini et al. 1983). Indeed, other than in reptiles with ESD, no groups of animals appear to have sex always determined solely in response to the environment. Thus the above definition masks this lability of sex determination and may even be misleading by identifying many different mechanisms of sex determination as ESD simply because some individuals have their sex determined in response to the environment. Thus, in the fish Menidia menidia it has recently been shown that some populations have only GSD while others have up to 80% of individuals with ESD (Conover and Heins 1987). The limitations of this definition of ESD are recognised by Bull himself (1983, p110) who allows that "the distinction between ESD and GSD is necessarily one of degree...".

Environmental Sex Determination (sensu Bull) is widely distributed throughout the animal kingdom, though with rare exceptions
it is apparently not common in any one group. Its existence has been reported in a marine worm, a variety of animal and plant nematode parasites, a small number of crustaceans, a small number of fish and a considerable number of reptiles, including all crocodilians, some turtles and some lizards. Multiple origins of the mechanism appear likely and a number of hypotheses have been put forward to explain the evolution and maintenance of the mechanism in reptiles (Charnov and Bull 1977; Thompson 1983; Webb and Smith 1984). However, its selective advantages remain obscure (Bulmer 1987). One model predicts that ESD and GSD could evolve from each other and that neither is a priori primitive to the other (Bull 1981b, 1983). To date, no species possessing heteromorphic sex chromosomes has been found to have ESD and it is reasonable to expect that, as suggested by Bull (1980), the two are incompatible.

1.3.2 INVERTEBRATES

A range of invertebrates are known to exhibit ESD. The best known examples are nematode worms of the Family Mermithidae and the marine echiurid worm *Bonellia viridis* (Bull 1983).

As larvae, Merthid nematodes parasitise insects, then emerge, to become free living adults, killing the host in the process (Christie 1929; Welsh 1965). The worm's size is apparently fixed by the time it leaves the host, and therefore its adult size is dependent solely on the amount of nutrition available to it while in the host. It has been shown that those nematodes with a relatively small amount of available food become male, whereas those with larger quantities of
available food become female. This relationship holds for differing
host sizes and differing levels of nourishment available to the host
(Christie 1929; Petersen 1972, 1977; Ezenwa and Carter 1975; Harlos et
al. 1980).

_Bonellia viridis_ is a free living marine worm (Phylum
Echiura), though adults are largely sessile with males being very
small and leading a parasitic existence on the female (Bacci 1965).
Sex is determined after larvae cease their planktonic existence and
settle on the substrate. Those individuals settling in isolation
generally become females whereas those settling on a female become
male (Bacci 1965; Leutert 1975). One study found sex to be unrelated
to environment in 17% of the larvae and thus the authors assumed sex
to be genetically determined in those individuals (Jaccarini et al.
1983). It has been suggested that sex determination in _Bonellia_ is
polyfactorial with some genotypes being sensitive to the environment
whereas others are not (Bacci 1965; Jaccarini et al. 1983). There has
been no empirical validation of the existence of polyfactorial sex
determination in _Bonellia_.

The crustacean _Ione thoracica_ is parasitic on fish and has a
pattern of sex determination similar to that of _Bonellia viridis_. The
animals are sexually undifferentiated as larvae. The first individual
to settle on the gills of a host fish becomes female while the second
becomes male (Bacci 1965). Two species of the amphipod genus _Gammarus_
are known to have sex determination sensitive to photoperiod. Of three
species in the genus, one shows a marked though variable relationship
between sex and photoperiod, a second shows a less marked relationship
and a third shows no relationship at all (Bulnheim 1978). Like the situation in Bonellia, sex determination in Gammarus may be polyfactorial (Bacci 1965). Numerous aquatic invertebrates exhibit skewed sex ratios and these cases may also reflect polyfactorial sex determination, with some genotypes being sensitive to temperature (Bacci 1965). Again, however, there has been no empirical validation of polyfactorial sex determination in any of these species.

1.3.3 VERTEBRATES

1.3.3.1 FISH

Conover (1984) suggests that ESD may be quite widespread among fish, though few have as yet been examined for its presence. ESD certainly occurs in the Atlantic Silverside, *Menidia menidia*, where sex is influenced by temperature with lower temperatures producing females (Conover and Kynard 1981; Conover 1984). Not all individuals have their sex determined in response to the environment, and the proportion which do so varies geographically (Conover and Heins 1987). Many cyprinodont fishes exhibit a mode of sex determination in which some putative genotypes are temperature sensitive (Bacci 1965; Sullivan and Schultz 1986).

1.3.3.2 AMPHIBIANS

Environmental Sex Determination is presently unknown among the Amphibia. The majority of species lack heteromorphic sex chromosomes and thus at least have the potential for ESD (Engel and
Schmid 1981; Schmid 1983). However, GSD is believed to be widespread (Schmid 1983).

Environmental sex reversal is known to occur in a number of amphibians. In the salamander *Pleurodeles waltlilii*, for example, high temperatures may produce a male which is genotypically female (Houillion and Dournon 1978; Zaborski 1986). Egg overripeness (delayed fertilisation) and the application of external hormones are also known to have the potential to affect sex determination (Bacci 1965; Bull 1983). Wallace (1984) suggests, on the basis of limited data, that ESD may occur in the crested newt, *Triturus cristatus*.

1.3.3.3 BIRDS AND MAMMALS

Heteromorphic sex chromosomes are generally considered to be ubiquitous among birds and mammals, thus making the existence of ESD in these groups most unlikely (Bull 1980). However, the presence of heteromorphic sex chromosomes among the ratites is a matter of debate (see de Boer 1980).

1.3.4 REPTILES

1.3.4.1 GENERAL

The distribution of ESD among reptiles is incompletely known, though the mode of sex determination has been suggested to be conserved at the subfamilial level (Bull et al. 1985). The mode of sex determination has been examined in two of the four reptilian orders.
Both ESD and GSD have been identified in the Orders Chelonia and Squamata, though Suborder Ophidia (Order Squamata) appears to have only GSD (Bull 1980, 1983; Olmo 1986). ESD has been found in all crocodilians thus far examined and is believed to be ubiquitous in this order (Webb and Smith 1984; Ferguson 1985). The Order Rhynchocephalia and Suborder Amphisbaenia (Order Squamata) have not been examined for the existence of ESD (Harvey and Slatkin 1982). Sex chromosomes are absent in both groups (Olmo 1986).

ESD is qualitatively different in reptiles when compared to its occurrence in other animals. It appears to be very common in some groups of reptiles and, when it occurs, all individuals have their sex determined in response to the environment.

1.3.4.2 ENVIRONMENTAL VARIABLES

ESD in reptiles was initially assumed to be Temperature-dependent Sex Determination (TSD), constituting a special case of ESD (Bull 1980). This terminology reflects the consistent use of temperature as the primary environmental variable in the examination of sex determination under laboratory conditions. However, there has been no evidence that temperature per se is related to sex determination or that temperature is the only environmental variable able to act as a trigger in sex determination (Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987). Thus, both substrate water potential, i.e. the amount of water available to the embryo (Gutzke and Paukstis 1983), and rate of development (Webb, Beal, Manolis and Dempsey 1987) have also been shown to be related to sex determination.
Of the various factors related to sex determination, it appears likely that embryo development rate is the best correlate of sex (Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987; Hutton 1987). As such, any environmental variable that affects the rate of embryo development may influence sex (Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987; Hutton 1987). This includes any variations in either egg structure or egg dimensions that modify its gaseous, hydric or thermal exchanges.

Even so, the majority of current studies consider temperature as the key environmental variable. Thus, in this thesis, temperature will be the primary factor under consideration.

1.3.4.3 GENETIC INFLUENCES

While ESD in reptiles describes the situation where sex is determined in response to the incubation environment, it, nonetheless, has a genetic basis, since it is a genetically determined mechanism which translates environment into sex. Moreover, the precise mode of operation of the environmental trigger apparently varies both within and between species and this variation may also have a genetic basis, although this has not been rigorously established. Thus, there may be two components to ESD, each of which may be operated upon separately by selective forces. Among reptiles, there is no evidence that the operation of the basic mechanism is constrained in any way, as is the case in Menidia menidia where some populations show ESD whereas others do not (Bulmer 1987; Conover and Heins 1987). Therefore, in reptiles it is the genetically determined form of the relationship between
environment and sex that may vary under the action of natural selection (Bull et al. 1982a, 1982b; Bulmer and Bull 1982).

Any investigation of the genetic influences on sex determination, and the mode of action of natural selection on those influences, necessarily centres on that range of temperatures over which sex ratio changes from one extreme to the other, and that precise temperature which produces a 0.5 sex ratio. Both the terminology and methodology employed in such investigations are in need of standardisation. In Appendix 1, it is recommended that those temperatures over which sex ratio changes be called the Transition Zone; that the breadth of that Zone be called the Transition Interval; and, that the temperature which produces a 0.50 sex ratio be called the pivotal temperature. Probit analysis is the technique recommended for the estimation of those parameters.

The limited available data for geographic variation in pivotal temperature and transition zone are also discussed in Appendix 1. Briefly, the data of Bull et al. (1982b) demonstrate a significant difference in pivotal temperature between Wisconsin and Tennessee populations of the turtle Graptemys pseudogeographica. However, the pivotal temperature is higher in Wisconsin than in Tennessee (+0.43 °C; Appendix 1), whereas the expectation in terms of ambient temperature in the two environments is that it should be lower (Bull et al. 1982b). There are two possible explanations for this result: (1) selection on maternal behaviour (nest site selection) leading to an overcompensation for differences in ambient temperature; and (2) the existence of a second (lower) pivotal temperature which is varying
Table 1.1. The distribution of environmental sex determination among reptiles. Sex versus temperature indicates the sexual phenotype with respect to increasing temperature.

<table>
<thead>
<tr>
<th>Group/Species</th>
<th>Sex versus temperature</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ORDER CHELONIA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SUBORDER Pleurodira</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>FAMILY Pelomedusidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Podocnemis expansa</td>
<td>F M ?</td>
<td>Alho et al. 1985</td>
</tr>
<tr>
<td><strong>SUBORDER Cryptodira</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>FAMILY Chelydridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chelydra serpentina</td>
<td>F M F</td>
<td>Yntema 1976, 1979</td>
</tr>
<tr>
<td>Macrochelys temmincki</td>
<td>F M F</td>
<td>Vogt et al. 1982</td>
</tr>
<tr>
<td><strong>FAMILY Kinosternidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kinosternon flavipes</td>
<td>F M F</td>
<td>Vogt et al. 1982</td>
</tr>
<tr>
<td>Sternotherus odoratus</td>
<td>F M F</td>
<td>Vogt et al. 1982</td>
</tr>
<tr>
<td><strong>FAMILY Emydidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chiromys rivingtoni</td>
<td>?</td>
<td>Hou Ling 1985</td>
</tr>
<tr>
<td>Chrysemys picta</td>
<td>F M F</td>
<td>Gutzke and Faukstis 1983</td>
</tr>
<tr>
<td>Emys orbicularis</td>
<td>M F</td>
<td>Pielau 1975a</td>
</tr>
<tr>
<td>Graptemys geographica</td>
<td>M F</td>
<td>Bull and Vogt 1979</td>
</tr>
<tr>
<td>G. pseudogeographica</td>
<td>M F</td>
<td>Bull and Vogt 1979</td>
</tr>
<tr>
<td>G. pulcra</td>
<td>M F</td>
<td>Bull and Vogt 1979</td>
</tr>
<tr>
<td>Pseudemys scripta</td>
<td>M F</td>
<td>Bull et al. 1982b</td>
</tr>
<tr>
<td>Emys blandingi</td>
<td>?</td>
<td>Vogt and Bull 1982</td>
</tr>
<tr>
<td>Terrapene sp</td>
<td>?</td>
<td>Vogt and Bull 1982</td>
</tr>
<tr>
<td><strong>FAMILY Testudinidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testudo graeca</td>
<td>M F</td>
<td>Pielau 1975a</td>
</tr>
<tr>
<td>Gopherus sp</td>
<td>?</td>
<td>Vogt and Bull 1982</td>
</tr>
<tr>
<td><strong>FAMILY Cheloniidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caretta caretta</td>
<td>M F</td>
<td>Yntema and Mrosovsky 1980</td>
</tr>
<tr>
<td>Chelonia mydas</td>
<td>M F</td>
<td>Miller and Limbus 1981</td>
</tr>
<tr>
<td>Eretmochelys imbricata</td>
<td>M F</td>
<td>Dalrymple et al. 1985</td>
</tr>
<tr>
<td>Lepidochelys olivacea</td>
<td>M F</td>
<td>Dimond and Mohanty-Hejmadi 1983</td>
</tr>
<tr>
<td><strong>FAMILY Dermochelyidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermochelys coriacea</td>
<td>M F</td>
<td>Rimblot et al. 1985</td>
</tr>
<tr>
<td><strong>FAMILY Carettochelyidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carettochelys insculpta</td>
<td>M F</td>
<td>Webb, Choquenot and Whitehead 1986</td>
</tr>
<tr>
<td><strong>ORDER Crocodylia</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SUBORDER Kusuchia</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>FAMILY Alligatoridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alligator mississippiensis</td>
<td>F M</td>
<td>Ferguson and Joanen 1982, 1983</td>
</tr>
<tr>
<td><strong>FAMILY Crocodylidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crocodylus johnstoni</td>
<td>F M F</td>
<td>Webb and Smith 1984</td>
</tr>
<tr>
<td>C. porosus</td>
<td>F M F</td>
<td>Webb, Beal, Manolis and Dempsey 1987</td>
</tr>
<tr>
<td>C. niloticus</td>
<td>F M</td>
<td>Hurtun 1984, 1987</td>
</tr>
<tr>
<td>C. palustris</td>
<td>F M F?</td>
<td>Lang, pers. comm.</td>
</tr>
<tr>
<td><strong>ORDER Squamata</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SUBORDER Sauria</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>FAMILY Agamidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agama agama</td>
<td>F M</td>
<td>Charnier 1966</td>
</tr>
<tr>
<td><strong>FAMILY Gekkonidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eublepharis macularius</td>
<td>F M</td>
<td>Wagner 1980</td>
</tr>
<tr>
<td>gekko japonicus</td>
<td>F M F</td>
<td>Tokunaga 1985</td>
</tr>
</tbody>
</table>
in the appropriate direction (Bull et al. 1982b). The former hypothesis is generally supported (Vogt and Bull 1982, 1984), and there is no evidence for a second pivotal temperature in *G. pseudogeographica*. However, a second pivotal temperature has been reported for *Chrysemys picta* which appears to vary geographically in the expected fashion (Schwarzkopf and Brooks 1985).

Bull et al. (1982a) demonstrated what they assumed to be significant variation in pivotal temperature within a population of *Graptemys ouachitensis*. However, given that the experiment was carried out at near the pivotal temperature and that only temperature was controlled, it is possible that other environmental variables were uncontrolled in the experiment (e.g. egg size, egg shell thickness).

The data of Limpus et al. (1983, 1985) for *Caretta caretta* (Appendix 1) certainly indicate that significant variation does exist in pivotal temperature. However, more extensive studies are required before the significance of that variation can be determined.

### 1.3.4.4 AVAILABLE LABORATORY AND FIELD DATA

The available information on ESD in reptiles is summarised in Table 1.1. Among crocodilians, ESD is best known in *Alligator mississippiensis*, *Crocodylus johnstoni*, and *C. porosus* (see, for example, Ferguson and Joanen 1982, 1983; Webb, Buckworth and Manolis 1983d; Webb and Smith 1984; Ferguson 1981, 1982, 1985, 1987; Joanen et al. 1987; Webb, Beal, Manolis and Dempsey 1987). Embryological development in the three species is remarkably similar up to the end
Fig. 1.1. The relationship between constant temperature incubation and sex ratio in *C. johnstoni* (a), *C. porosus* (b) and *A. mississippiensis* (c). Data from Webb, Beal, Manolis and Dempsey (1987) and Ferguson and Joanen (1982, 1983). Open circles indicate a coincidence of data points.
of organogenesis. Alligators, however, hatch at an earlier embryological stage than do crocodiles and hence are less mature at hatching (Ferguson 1985, 1987; Webb, Beal, Manolis and Dempsey 1987).

With *C. johnstoni* and *C. porosus*, incubation in the laboratory at high (>33°C) and low (<30°C) temperatures results in females; males are produced at intermediate temperatures (30.5-32.5°C) (Fig 1.1). In contrast, *A. mississippiensis* produces females at low temperatures (< 30.0°C) and males at high temperatures (≥ 34.0°C; Fig. 1.1). *C. johnstoni* apparently differs from the other two species in that no constant temperature produces 100% males (Fig. 1.1); females are produced at all temperatures thus far tested at which survival is possible, though at varying frequencies (Webb, Beal, Manolis and Dempsey 1987). The data for *C. porosus* are, at this stage, equivocal and this species too may prove not to produce all males at any constant temperature (see Webb, Beal, Manolis and Dempsey 1987).

Field data for *C. johnstoni* indicate that some nests do produce exclusively males, thus demonstrating a significant difference between laboratory and field results (Webb and Smith 1984). The nests of *C. johnstoni* experience marked diurnal temperature fluctuations and an increasing mean nest temperature during incubation, both of which may be related to the observed discrepancies between laboratory (constant temperature) and field (fluctuating temperature) results (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984). The larger, thermally more stable, nests of *A. mississippiensis* and *C. porosus* do not experience pronounced diurnal temperature variation and there is far better agreement between laboratory and field observations for
these species, especially in the case of *A. mississippiensis* (Ferguson and Joanen 1982, 1983).

Among turtles, females are generally produced at high temperatures and males at low temperatures (Table 1.1). However, where one sex is produced at both high and low temperatures, it is always female. On the basis of parsimony, this supports the contention that the primitive relationship between increasing temperature and sex in reptiles with ESD is female, male, female, and that any other distribution arises from the loss of either high temperature or low temperature females (Webb and Smith 1984).

The precise relationship between temperature and sex determination is extremely complex. Webb, Beal, Manolis and Dempsey (1987) found that for *C. johnstoni*, some embryos are sensitive to temperature perturbations from within the first few days of incubation and until some 65% of incubation, depending on the temperature concerned. The period of incubation during which *C. porosus* embryos are sensitive to temperature is contracted compared to that in *C. johnstoni* (Webb, Beal, Manolis and Dempsey 1987). In both species the precise embryological period during which sex determination is sensitive to incubation temperature is itself temperature dependent. Sex determination in turtles with ESD is similar to that in crocodilians, in that the temperature sensitive period is in the middle third of incubation (Yntema and Mrosovsky 1982; Raynaud and Pieau 1985). Contrary to expectation, sex in crocodiles and turtles is determined at a later embryological stage in rapidly developing (high temperature) embryos than in slowly developing (low temperature)
embryos. The same is not true of *Menidia menidia*, where sex is fixed earlier in embryos developing at higher temperatures (Conover and Fleisher 1986).

In *A. mississippiensis* it is now known that post-hatching growth and survival are both related to the incubation environment, and in particular to the temperature (Joanen et al. 1987). Sex and survivorship of field embryos of *C. johnstoni* and *Chrysemys picta* are also known to be related (Webb and Smith 1984; Schwarzkopf and Brooks 1985). Females, in selecting nest sites, are believed to choose those environments which maximise survival (Webb and Smith 1984; Schwarzkopf and Brooks 1987). These sites also lead to a higher probability of the production of males (Webb and Smith 1984). The relationship between sex and survivorship observed in *C. johnstoni* appears to hold also for *Chrysemys picta*.

1.3.5 THE PROPOSED MOLECULAR BASIS OF ENVIRONMENTAL SEX DETERMINATION

The molecular basis of ESD, like that of GSD, is unknown (Standora and Spotila 1985). The H-Y antigen (histocompatibility-Y; serologically detectable male, SDM) has been implicated in primary sex determination (Wachtel et al. 1975b; Silvers et al. 1982) although the nature of its role remains contentious (Goodfellow and Andrews 1982; Standora and Spotila 1985). This antigen is highly conserved among different animal groups (Wachtel et al. 1975a; Muller and Wolf 1979) and, with one exception (the turtle *Siebenrockiella crassicollis*, Engel et al. 1981; Carr and Bickham 1981), is always associated with the heterogametic sex.
The H-Y assay can pose problems, and one case exists of conflicting H-Y typings (the X* form of the wood lemming *Myopus schisticolor*, Wachtel et al. 1976; Wilberg et al. 1982). In this case, it is unclear whether the conflicting results are an artefact of differing methodologies or simply the reflection of unrecognized heterogeneity in the system under study (Goodfellow and Andrews 1982). Moreover, methodological problems may be the cause of the discrepancy between the karyotype and H-Y typing of *Siebenrockiella crassicollis* (Wellins 1987). However, it is possible in species which have recently evolved a chromosomal sex determination mechanism, that the H-Y antigen is not associated with the heterogametic sex (Nakamura et al. 1984). Even so, the overwhelming majority of studies on H-Y support its fundamental role in primary sex determination (Wachtel 1983).

The detailed study of H-Y in species with ESD is limited (Standora and Spotila 1985), although many species have now been typed (Engel et al. 1981; Wellins 1987; Nakamura et al. unpublished). An extensive study of *Emys orbicularis* showed that the gonads of males typed H-Y negative whereas the gonads of females typed H-Y positive (Zaborski et al. 1982). Serum H-Y showed no association with sexual phenotype but rather was found to be randomly distributed with an H-Y positive frequency of approximately 50%. The authors concluded that the female was the heterogametic sex and that the gonad H-Y reflected sexual phenotype while serum H-Y reflected sexual genotype (Zaborski et al. 1982). These results strongly suggest that ESD in reptiles may depend on environmental sex reversal as suggested by Engel et al. (1981). Similar results have been generated in a limited study of *A. mississippiensis* (Nakamura et al. unpublished).
This finding is apparently in conflict with the theoretical expectation that the transition from GSD to ESD should be accompanied by the complete loss of heterogamety (Bull 1980, 1983). However, the distribution of heteromorphic sex chromosomes in turtles suggests that these chromosomes are of recent and independent origin (Bull 1980, 1983). It may be that GSD evolved from ESD in turtles and it is possible that, in such a case, there could be heterogamety with environmental override. The results for *E. orbicularis* could be consistent with a species undergoing the transition from ESD to GSD. This, however, is a topic on which far more research is required before any firm conclusions can be drawn.

The conserved nature of the Banded krait minor (Bkm) satellite DNA sequence in animals (Singh et al. 1979, 1981; Jones and Singh 1981a, 1981b; Singh and Jones 1982) and its possible relationship to sex determination in reptiles led Standora and Spotila (1985) to propose the existence of similar specific sex determining satellite DNA sequences in turtles. The role of such sequences in sex determination and their suggested conservation has, however, been called into question (Levinson et al. 1985; Schaffer et al. 1986a, 1986b; John 1987), and it appears now that the role attributed to them by Singh, Jones and co-workers is incorrect. Thus, the importance attributed to such sequences (Spotila and Standora 1985) can be discounted.
1.3.6 THE PROPOSED THEORETICAL BASIS OF ENVIRONMENTAL SEX DETERMINATION

Numerous theories have been proposed to account for labile sex determination (Bull 1981b). With respect to ESD in reptiles, three have been suggested but only one has been extensively developed.

Thompson (1983) proposed that ESD functions to maintain gene flow by producing single sex clutches that could not interbreed so that crossbreeding became mandatory. This claim has received little support: mixed sex clutches are common among animals with ESD (Webb and Smith 1984; Ferguson and Joanen 1982, 1983). Moreover, the hypothesis would require that a given female consistently produce only one sex or the other, which is not supported by observation (Schwarzkopf and Brooks 1987).

Webb and Smith (1984) argued that ESD may be intimately related to embryo survivorship. The hypothesis required that the time of sexual differentiation be constrained by demands on the mesonephric kidney, since it is from the anterior portion of the kidney primordium that the gonad is partitioned. In particular, rapidly developing embryos were assumed to be under metabolic stress and might have their survivorship compromised if programmed to develop a gonad early in development. This hypothesis implied that the coupling of the timing of gonadal differentiation to the environment evolved in response to general survivorship considerations and that the relationship between sex and environment resulted from different selective forces (see Charnov, 1982, for a discussion of sex allocation theory). The
hypothesis was derived from studies of field and laboratory incubation of *Crocodylus johnstoni* (Webb and Smith 1984). It is supported by the lack of negative evidence and the apparent failure of the predictions of alternative hypotheses (Hutton 1987).

Charnov and Bull (1977) outlined a model for the evolution and maintenance of ESD, which has subsequently been extensively developed (Bull 1981a, b, 1983; Bulmer and Bull 1982; Charov and Bull 1985). The model states that, in reptiles, ESD will be selected for when the incubation environment affects the fitness of the resulting animals in a profound and sexually dimorphic manner. Put simply, the incubation environment is expected to have a far greater impact on the relative fitness of one sex than on the other. As such, some environments may, for example, produce males of high fitness and females of average fitness while another environment may produce low fitness males and average fitness females. Those environments would, therefore, produce males and females respectively. As currently interpreted for crocodilians, incubation environment is a determinant of post-hatchling growth and survival, with large size being a more important correlate of fitness for males than for females (Joanen et al. 1987; Webb, Beal, Manolis and Dempsey 1987).

The general Charnov-Bull model has support from a number of studies on invertebrates (see Charnov and Bull 1977; Bull 1983), the fish *Menidia menidia* (Conover 1984; Conover and Heins 1987), and one reptile, *Alligator mississippiensis* (Harvey and Partridge 1984; Joanen et al. 1987). It is unclear whether in this model ESD precedes GSD, but it has been shown theoretically that either could evolve from the other.
1.4 THE SUITABILITY OF *Crocodylus johnstoni* AS AN EXPERIMENTAL ANIMAL

*Crocodylus johnstoni* is particularly amenable to population studies (Webb and Smith 1984, 1987; Smith and Webb 1985). Its selection as an experimental animal for this study depends on three factors: (1) the existence of a well studied population; (2) the existence of a study area which is accessible, contains a sufficiently large population, and in which the time and location of nesting are well known; and (3) the fact that the species nests within a short time and often nests in colonies. An additional advantage of using *C. johnstoni* is the growing volume of data from laboratory and field studies on sex determination (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987) and embryo physiology and ecology (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987; Webb, Manolis, Dempsey and Whitehead 1987; Webb, Manolis, Dempsey and Whitehead 1987; Manolis, Webb and Dempsey 1987; Whitehead 1987a, b).

The major drawback in using *C. johnstoni* is the impossibility of following animals from hatching to maturity due to the long periods of time required (10-15 years). This problem is common to a majority of reptiles with ESD. Indeed, the fitness of individual animals cannot be objectively determined, and so can only be inferred from general observations on adult crocodiles.
1.5 AIMS OF THIS STUDY

As has been shown, our knowledge of Environmental Sex Determination in vertebrates is growing rapidly - particularly in a laboratory setting. What are lacking, however, are the data sufficient to allow the integration of ESD into our understanding of the ecology of the animals concerned. The most extensive studies already completed (Webb and Smith 1984; Schwarzkopf and Brooks 1985, 1987) have been limited, and their relevance to arguments concerning the evolution and maintenance of ESD is unclear. Indeed, it has yet to be determined whether detailed ecological studies can provide any insight into such arguments, or whether comparative studies are better suited to this purpose.

The broad aim of the present study is to provide sufficient ecological data to evaluate ESD in terms of the population structure and dynamics of the McKinlay River area population of the Australian Freshwater Crocodile, C. johnstoni. To date, only the study of Webb and Smith (1984) has considered the possibility that ESD may be intimately related to population dynamics. Most attention has been drawn to the expectation that ESD operates in crocodilians such that an individual's growth potential is determined by their incubation environment and that those environments which bestow the maximal growth potential are also those which produce males (Webb, Beal, Manolis and Dempsey 1987). An examination of the influence of incubation environment on the pattern of growth to adulthood is outside the scope of this study. Rather, this study addresses that period of time from the onset of the C. johnstoni nesting season to
such time as hatchlings have endured up to one month of post-hatching life. The central theme of the study is to determine whether there is a relationship between population structure/dynamics and the operation of ESD. In the Chapters that follow, this theme will be explored through the following five questions:

1. Do females select nests sites with reference to environmental cues, and if so, which cues (Chapter 4);
2. Within a nesting season, is there an ordering of females with respect to time of nesting (Chapter 4), and if so, is there an association between time of nesting and the sex ratio of the resulting embryos (Chapters 4 and 5);
3. What environmental correlates of hatchling sex ratio exist, and when and in what fashion do they operate (Chapter 5);
4. What environmental correlates of embryonic survival exist, and are they the same as those correlates of hatchling sex ratio (Chapter 5); and
5. Is hatchling survival random, and if not, what phenotypic correlates of survival exist, and does hatchling survival relate in some way to the incubation environment (Chapter 6).

The answers to the above questions can be expected to provide an insight into the dynamics of nesting, embryonic survival, sex determination, and hatchling survival in *C. johnstoni*.

In each Chapter where data relating to these questions is provided, the individual results are presented without discussion. The relevant discussion appears at the end of each of the Chapters. Given
that there is a considerable number of Tables and Figures associated with the text that follows, it was decided that, rather than disrupt the text by interspersing the Tables and Figures, they should all appear at the end of the relevant Chapter. Tables appear before Figures.
CHAPTER 2

THE MCKINLAY RIVER AREA

AND ITS CROCODYLUS JOHNSTONI POPULATION

2.1 GENERAL

Crocodylus johnstoni Krefft, 1873, is the only extant crocodilian species restricted to the Australian mainland (Cogger et al. 1983). The habitats it occupies include the rivers, streams and pools (billabongs) which drain the north coast of the Australian mainland (Worrell 1952, 1970; Cogger 1979; Fig. 2.1). Whilst occurring primarily in fresh water, C. johnstoni may also be found in saline areas (Messel et al. 1981; Webb, Manolis and Sack 1983). It possesses functional lingual salt glands capable of excreting concentrated salt solutions, enabling it to survive in very saline areas (Taplin et al. 1982). However, it appears likely that C. johnstoni is excluded to some extent from these areas by C. porosus (Messel et al. 1981; Webb, Manolis and Sack 1983).

Crocodylus johnstoni is a relatively small crocodilian and is well suited to demographic study because: it is abundant (Groombridge 1982; Webb, Manolis, Whitehead and Letts 1984); it is neither endangered nor threatened (Jenkins 1979; Burbidge 1987; Taplin 1987; Webb, Whitehead and Manolis 1987); individuals congregate in high densities during annual dry seasons (Webb, Manolis and Buckworth 1983); and, they nest within a contracted period (Webb, Buckworth and Manolis 1983d). By virtue of its small size, it is comparatively easy

2.2 THE MCKINLAY RIVER STUDY AREA

2.2.1 THE GENERAL STUDY AREA

The M'Kinlay River study area of Webb and co-workers extends from 12°46'S to 13°21'S at approximately 131°51'E (Webb, Manolis and Buckworth 1983). It covers some 100-150 km² adjacent to the mainstream (Fig. 2.2). Story et al. (1969) describe the area as quaternary alluvial plains of variable nature consisting of channels and floodplains. Soils include uniform sands and silts, gradational acid loamy and sand soils, gradational alkaline loamy soils, and alkaline texture-contrast soils.

Vegetation types include: paperbark forests of Melaleuca leucadendron, M. cajaputi, and/or M. viridiflora in a dominant, broken or unbroken canopy; tall and mid-height grassland of Themeda sp., Chrysopogon sp., Cyperaceae, Eriachne burkittii, annual Sorghum sp., Heteropogon triticeus, Panicum delicatum, Ectrosia sp., Ischaemum sp., and Eragrostis sp.; and savannah consisting of tall and mid-height grassland with an overstorey of Eucalyptus papuana, E.
polycarpa, E. apodophylla, E. alba, E. calvigera, E. latifolia, Pandanus spp. and Melaleuca spp.. The trees Pandanus spp. and Melaleuca spp. are a conspicuous feature of the fringing vegetation of most water bodies, as is bamboo, Bambusa arnhemica, along the mainstream and major creeklines (Storey et al. 1969).

2.2.2 CLIMATE

The climate of the study area is markedly seasonal (Table 2.1). The dry season (April-November) is characterised by little rainfall (approximately 20% of the annual total) and evening temperatures that are relatively low. During this period, the McKinlay River mainstream ceases to flow and contracts to small pools isolated by large expanses of dry river bed. Water levels drop throughout the study area during the dry season. The wet season (December-March) brings the bulk of rains, and widespread flooding is common throughout the study area in the peak of the wet season (February) (Webb, Manolis and Buckworth 1983).

2.2.3 MAJOR STUDY SITES

Within the general study area, seven pools represent major Sites for the present study. All pools were within 500 m of the mainstream, and were within 18 river kilometers of the McKinlay River/Mary river junction (Fig. 2.2). The basic parameters of the pools are given in Table 2.2. Fig. 2.3 shows an aerial view of Site Two and Fig. 2.4 shows an aerial view of a section of Site 4. These views are typical of the two general forms of floodplain pool found in
the area: the broad shallow pool and the deep long channel respectively.

The pools are numbered in a southerly sequence. Additional to the downstream pools, nests were located at four pools further upstream. As these pools contributed only five *C. johnstoni* nests in 1983, one in 1984 and were not examined in 1985, the sites will neither be individually identified nor described. They will be referred to as the Upstream Sites.

2.2.3.1 SITE ONE

Site One is particularly important as it was used for hatchling survival experiments (Chapter 6). Like Sites Six and Seven, it lies on the West bank of the McKinlay River (Fig 2.4). The pool is connected to the mainstream by a 40 m long gully which drops some 4 m in height. For most of the dry season, the pool is effectively subdivided into two pools, one long and narrow, the other short and wider.

2.2.3.2 SITE TWO

Site Two lies on the East bank of the McKinlay River. Irregular in shape, it consists of a large, open, shallow section and a smaller narrow, overgrown deeper channel. The pool has a small population of *C. johnstoni* (Table 2.1) and consequently generates little nesting activity.
2.2.3.3 SITE THREE

This is the most important of the Sites in the study area. The main pool is large, oval in shape and shallow (<2 m mid-dry season). Associated with this pool is an extensive (1.3 km) creek system which although generally narrow (<10 m) is considerably deeper (up to 3 m) than the main pool.

This Site harbours has a considerable crocodile population (Table 2.1) and is the location of concentrated colonial nesting. The Site has undergone considerable change since first examined in 1978. Those relating to the nesting bank are briefly described in Chapter 4, but general changes include a siltation of the pool with a resulting reduction in depth. This appears to have lead to the bulk of the *C. johnstoni* population spending most of the dry season in the creek system associated with the pool. Casual observations based on spotlight surveys of the pool suggest that the crocodiles move into the main pool during the nesting and hatching periods but otherwise are generally absent.

2.2.3.4 SITE FOUR

Site Four consists of one reasonably large pool and an extensive series of channels; a section of which appears as Fig. 2.4. The *C. johnstoni* population is not large (Table 2.1), and the Site produces only a low number of nests (Table 2.1).
2.2.3.5 SITE FIVE

This is the smallest of the pools, yet it has the highest crocodile population (Table 2.1). The pool has much nesting behaviour associated with it. However, most females do not nest on the margin of the pool itself, but rather in the adjacent McKinlay River mainstream, 30 m to the West. Early in the dry season, the majority of the crocodiles which will subsequently occupy Site Five are in pools within the adjacent mainstream but, as these contract and finally vanish, the crocodiles move into Site Five.

2.2.3.6 SITE SIX

Site Six is a small, oval pool on the west bank of the McKinlay River. It has a small C. johnstoni population (Table 2.1) and this is reflected in a low nesting effort (Table 2.1). The nesting that does take place occurs in a creek 40 m North of the pool and which connects to both Site Seven (to the west) and to the mainstream (to the east). It is possible that the nesting bank is used by crocodiles from both Sites Six and Seven.

2.2.3.7 SITE SEVEN

Site Seven is a large, deep pool (Table 2.1) on the west bank of the McKinlay River. The pool contains few crocodiles (Table 2.1) and nesting effort is consequently low. Given its size, the C. johnstoni population is unusually low (see Section 2.3.2). However, observation indicates that it is the Site in the study area most...
affected by human visitation (primarily wild pig hunters), and thus the low \( C. johnstoni \) may partly result from disturbance.

2.3 THE POPULATION AND ITS DISTRIBUTION

2.3.1 POPULATION SIZE

From spotlight surveys conducted in July and September 1979, it was estimated that the total McKinlay River \( C. johnstoni \) population was between 826 and 1156 individuals with a mean estimate of 963 (Webb, Manolis and Buckworth 1983). Surveys conducted in July 1983 found 369 individuals in areas which has yielded 390 crocodiles in July 1979 (Smith and Webb 1985). By extrapolation, the total 1983 McKinlay River population can be estimated as 911 individuals. It should be noted that this decline in population size is a result of research activities and thus does not represent a natural decline (Smith and Webb 1985). The population is believed to have a natural rate of increase of approximately 1.5% per annum (Smith and Webb 1985).

2.3.2 DRY SEASON DISTRIBUTION

In July and September 1979, 982 separate water bodies, greater than 2 m total length, were surveyed (Webb, Manolis and Buckworth 1983). Of those, 72.4% were mainstream pools, 23.4% were floodplain billabongs and 4.1% were swamps. Of all \( C. johnstoni \) sighted, 97.8% were in pools >1 m deep, and of those 22.3% were found in pools 1-2 m deep, and the remaining 77.7% in pools >2 m deep. Of the 982 pools surveyed, 85 were found to contain \( C. johnstoni \).
The relationship between pool depth and crocodile presence was modified by pool size. Of all pools >1 m deep, those with a size of >60 m (size was computed as the square root of length times width) were generally acceptable to crocodiles, with 69-80% occupancy. Pools with a size of 31-60 m were marginally acceptable with an occupancy of 32%, and pools <30 m were generally unacceptable. Similar trends were noted with respect to the numbers of crocodiles sighted in each pool.

2.3.3 WET SEASON DISTRIBUTION

Little is known of C. johnstoni ecology during the annual wet season other than that many do not remain in their dry season refuges. Webb, Manolis and Buckworth (1982) noted that in the Mary river, the majority of animals appear to remain at the water's edge and hence disperse over the flood plain with rising flood waters. Observations in both the McKinlay- and Adelaide rivers suggest a rapid dispersal from dry season refuges with the first wet-season rains (Webb, Buckworth and Manolis 1983a).

2.4 GROWTH, MOVEMENT AND THE POPULATION STRUCTURE

2.4.1 GROWTH

Crocodylus johnstoni is a small crocodilian. Hatchlings average 24.4 cm in total length in the McKinlay River population and males grow to an estimated total length of 3 m (Webb, Buckworth and Manolis 1983a, d). Maximum age attained is at least 45 years (Webb, Buckworth and Manolis 1983a; Webb and Smith 1984; Smith and Webb 1985).
Growth rate is more closely related to age than is size and generally declines throughout life. The age-size relationship of individuals can be adequately modelled by two exponential curves and a method for correcting for individual variation in growth rate has been derived (Webb, Buckworth and Manolis 1983a). Sexual dimorphism and an additional size dimorphism due to location in the study site (upstream versus downstream) are apparent only in animals greater than five years of age (approximately 1.2 m total length). The nature of the dimorphisms are such that females grow more slowly than males and upstream animals grow more slowly than downstream animals. The difference between upstream and downstream may relate to food availability (Webb, Buckworth and Manolis 1983a; Webb 1985).

2.4.2 THE POPULATION AGE AND SEX STRUCTURE

Webb, Buckworth and Manolis (1983a) and Smith and Webb (1985) derived the age structure of a sample of one quarter of the McKinlay River C. johnstoni population. This sample was assumed to provide an adequate estimate of the population age structure. An important feature of the population age structure was that the sex ratio was consistently skewed towards females, although the extent of the skew was variable. The population sex ratio was 0.33 in 1979 (expressed as the proportion of males in the population; Fig. 2.5) in a sample of 697 individuals. The sex ratio of hatchling cohorts is believed to vary at least between 0.12 and 0.46 (Webb and Smith 1984; Smith and Webb 1985).
The sex ratio among adults is 0.17, and that among juveniles is 0.37 (Webb, Buckworth and Manolis 1983a). This difference is statistically significant, although the reasons for the difference are unclear. Possible explanations include: social exclusion of males once maturity is reached; past hunting having been selective towards males (Webb, Buckworth and Manolis 1983a); and, a change in the recruitment sex ratio.

2.4.3 SURVIVORSHIP

Webb and Smith (1984) and Smith and Webb (1985) derived estimates of rates of survival for all *C. johnstoni* age classes. The hatching rate of all eggs laid is estimated to vary annually between 14.5% and 44.5% with a mean of 29.5%. The survivorship of hatchlings to one year of age is considered to vary between 7% and 17% with an average of 12%. Between one and ten years of age, the survival is rate estimated to be 85% per year. Survival of animals greater than ten years of age, but less than 30 years of age, is very high and is thought to approach 100% (Smith and Webb 1985). Survival of animals greater than 30 years of age is thought to steadily decline with age, and mean annual rates of survival are probably around 85% per year (Smith and Webb 1985).

2.4.4 MOVEMENT

Many *C. johnstoni* appear to move out of their dry-season refuges with the rising wet-season flood waters. Recapture rates from one dry season to another, however, are high. For a sample of 252
individuals marked and released in the dry season of 1978, 61.5% were recaptured once, and 20.2% twice in the two subsequent dry seasons. Of those recaptured, 83.4% were recaptured within one kilometre of the original capture site (Webb, Buckworth and Manolis 1983a). Of those C. johnstoni which had moved, more moved upstream than moved downstream, males and females moved to the same extent, younger crocodiles tended to move more than older ones, and crocodiles in the upstream section of the study area moved more than did those in the downstream section (Webb, Buckworth and Manolis 1983a). The tendency for individuals to be found in the same pool from one dry season to the next has been partially attributed to the well developed homing ability demonstrated to exist in this species (Webb, Buckworth and Manolis 1983b).

2.5 DIET AND FEEDING

C. johnstoni of all sizes feed almost exclusively on aquatic and terrestrial insects, fish and crustaceans. Primarily an opportunistic feeder, C. johnstoni mainly feeds at the vegetation/water interface (Webb, Manolis and Buckworth 1982). Prey size increases significantly with crocodile size. Also, with increasing crocodile size there is a shift from terrestrial to aquatic prey.

C. johnstoni is a seasonal feeder, with only 5.9% of crocodiles examined in the wet season having empty stomachs compared with 19% in the dry season. Furthermore, in the wet season there was an average of 16.2 prey items per crocodile compared with 1.8 in the
dry season. Cannibalism is known to occur in *C. johnstoni*, although only through anecdote.

2.6 REPRODUCTION

2.6.1 SIZE AND AGE AT MATURITY

Female *C. johnstoni* in the McKinlay River area may mature as early as nine years of age, although the majority mature at about 12 years of age; approximately 1.5 m total length (Webb, Buckworth and Manolis 1983d).

Males mature later, with the youngest known mature male being 13 years old (Webb, Buckworth and Manolis 1983a). On the basis of limited data, Webb, Buckworth and Manolis (1983a, d) consider the average age at male maturity to be 16-17 years; about 1.7 m total length.

2.6.2 COURTSHIP AND MATING

Compton (1981) observed courtship among captive *C. johnstoni* in north Queensland. It occurred episodically over 23 days, ceasing abruptly some six weeks before nesting was observed. Courtship extended for two to 26 minutes and was usually initiated by the male swimming slowly to the female and touching her snout with his. It involved snout-lifting, mutual jaw rubbing, submerging and bubbling; all behaviours known to occur in *A. mississippiensis* (Garrick and Lang 1977; Garrick et al. 1978). The male subsequently rubbed his throat
along the head of the female and climbed on her back. The male then moved his hindquarters down beside the female’s and inverted his tail while the female lifted hers. Copulation was not actually observed, but was assumed to have taken place (Compton 1981).

Neither courtship nor mating have been observed in wild C. johnstoni. Webb, Buckworth and Manolis (1983d) maintained a daily watch on a McKinlay River billabong in July and August 1979, but did not observe any courtship behaviours. On the basis of Compton’s findings it is likely that courtship had ceased before the observations began (Webb, Buckworth and Manolis 1983d).

2.6.3 NESTING

Like mating, nesting has yet to be observed among wild C. johnstoni, although it has been both observed and filmed with captive individuals. In the McKinlay River area, nesting occurs mainly in the last two weeks of August and the first week of September. Nesting is preceded by a period of two or three weeks during which females excavate in sand and other friable substrates adjacent to the pools. Approximately 84% of females greater than 11 years of age and 8% of females less than 11 years of age nest each year (Smith and Webb 1985).

The nest itself is a simple hole excavated in the substrate - usually sand (Webb, Buckworth and Manolis 1983d). The majority of nests have a distinct ovoid egg chamber with mean dimensions of 19.5 x 14.1 x 12.8 cm high. The top egg is on average 19.6 cm below
the surface. Mean clutch size in the McKinlay River area is 13.2 eggs (N=86 clutches), and mean egg dimensions are 6.64 x 4.19 cm with a weight of 68.2 g (Webb, Buckworth and Manolis 1983d).

Egg weight tends to increase significantly with clutch size, and total clutch weight tends to decrease through the nesting season. These two results suggest that larger females lay relatively large clutches of large eggs, and that larger females nest earlier in the nesting season than do smaller ones (Webb, Buckworth and Manolis 1983d).

Additional to observations of courtship, Compton (1981) observed nesting. A female dug a hole approximately 25 cm deep, into which 20 eggs were deposited. The hole was dug with the hind feet, which alternated with about one scratch per second. Digging would continue for up to five minutes, after which the crocodile would lie still, as if resting. Unfortunately, the time period over which the nest was dug was not recorded. During the 65 days following nesting, the female visited the nest site five times (Compton 1981). The purpose of such visits is unknown.

2.6.4 EMBRYO ECOLOGY

When laid, a C. johnstoni egg typically contains an embryo at the 10 - 20 somite stage (Ferguson 1985, 1987; Webb, Manolis, Dempsey and Whitehead 1987). Thus, crocodilian embryos are at a more advanced stage at laying than are the embryos of chelonians, rhynchocephalians and birds, but less advanced than the majority of snakes and lizards
(Webb, Manolis, Dempsey and Whitehead 1987). The egg is covered with a slimy gel or mucus (Ferguson 1985) which dries within one to two days of laying.

Within the egg, the embryo is attached to the inside of the vitelline membrane, and the yolk rotates immediately after laying such that the embryo is brought to the uppermost point of the egg (Webb, Manolis, Dempsey and Whitehead 1987; Webb, Manolis, Whitehead and Dempsey 1987). Should the embryo be at the exact bottom of the egg when laid, the yolk rotation mechanism may fail and the embryo will die (Webb, Manolis, Whitehead and Dempsey 1987). Within 24 hours of laying, the albumen above the embryo is dehydrated and the embryo attaches to the inside of the egg-shell membrane (Webb, Manolis, Dempsey and Whitehead 1987).

At the time of laying, the mass of the egg is composed of 11.9% egg shell and membranes, 46.0% yolk and 42.1% albumen (Manolis et al. 1987). However, shortly before laying, the embryo has started to remove water from the adjacent albumen, and deposit it within the vitelline membrane. This dehydration of the albumen accelerates after laying and causes changes in the structure of the egg shell. It becomes opaque in the areas overlying where albumen is being dehydrated, and initially this is directly above the embryo. As the dehydration increases, so the opacity spreads, firstly as a band, encircling the egg 3-4 days after laying, and stabilising in width by about 7 days (Webb, Manolis, Dempsey and Whitehead 1987; Webb, Manolis, Whitehead and Dempsey 1987).
This stable band remains until half of the total development has been achieved. Then, as the chorio-allantois spreads around the inside of the egg, dehydrating the remaining albumen, the opaque area spreads from the band to the poles of the egg; the egg becomes uniformly opaque. The opacity of the egg shell probably functions to enhance respiratory gas exchange across the egg shell (Ferguson 1982; Thompson 1985; Webb, Manolis, Dempsey and Whitehead 1987; Webb, Manolis, Whitehead and Dempsey 1987). Detailed studies of the respiration, embryonic development and chemistry of *C. johnstoni* development have been conducted (Manolis et al. 1987; Whitehead 1987a, b) but will not be considered further here.

*C. johnstoni* embryos have their sex determined by the incubation environment (Webb et al 1983d, Webb and Smith 1984). Temperature is the primary determinant of sex, but this does not exclude an influence of temperature on metabolic rate or rate of development which may itself be more directly linked to sex determination (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987). Under precisely controlled constant temperature incubation, exclusively female individuals arise between 26.0°C and 30.5°C and between 32.5°C and 34°C, while both males and females arise between 31.0°C and 32.0°C (Webb, Beal, Manolis and Dempsey 1987). To date, no constant temperature incubation regime has produced exclusively males (Webb, Beal, Manolis and Dempsey 1987). From limited data on field nests, both males and females arise from nests with total incubation times between 65 and 91 days, although there is a well defined peak of males between 70 and 80 days (Webb and Smith 1984).
Webb, Buckworth and Manolis (1983d) found that 2-4% of all eggs are infertile, or show no sign of embryo development. Webb and Smith (1984) examined the pattern of embryo survivorship among a sample of natural nests. Their finding that survivorship and sex are not independent is important in the examination of environmental sex determination. Differential survivorship with respect to sex was identified, but it operates in an unexpected fashion. Rather than embryonic females having a lower survivorship, it was shown that eggs which have a lower probability of survivorship become female because the probability of survival is largely fixed before the time of sex determination.

Additionally, Webb and Smith (1984) found that the most commonly selected nest temperature was that which gave a 0.49 sex ratio, suggesting that selection was operating to produce a 0.50 hatchling sex ratio. Moreover, those nest environments which produced a near 0.50 sex ratio also exhibited maximal embryo survivorship. However, to maximise overall embryo survivorship requires the production of a female biased sex ratio, suggesting that sex ratio selection is constrained by survivorship considerations.

2.6.5 HATCHING

Hatching of *C. johnstoni* in the McKinlay River area typically occurs in late October and throughout November (Webb, Buckworth and Manolis 1983d). Adults excavate the nests when hatchlings begin calling, and are known to assist hatching by excavating with their front legs or jaws and carrying the young to the water in their mouth.
There is no evidence that *C. johnstoni* hatchlings can escape the nest unaided. Creches of hatchlings are maintained for at least 1-2 weeks after hatching, usually with a larger crocodile in attendance.

### 2.7 PREVIOUS UTILISATION AND RESEARCH INFLUENCES

#### 2.7.1 HUNTING

The McKinlay River *C. johnstoni* population was extensively hunted between 1960 and 1963, and the size of the population prior to hunting is unknown. Smith and Webb (1985), from discussions with hunters suggest an initial population of about 2000 individuals. There is no evidence of hunting occurring during the period 1978-1985.

#### 2.7.2 RESEARCH INFLUENCES

Experimental manipulation of the population occurred between 1979 and 1983. A total of 2026 eggs and 30 individuals of various ages were removed from the population. Over the same period, 71 hatchling, 79 six month old, and 34 one year old animals were released into the population. These manipulations resulted in an estimated 5.4% decline in the population between 1979 and 1983 (Smith and Webb 1985).
Table 2.1. Meteorological data from Middle Point, 50 mk north-west of the study area. Data accumulated over at least 15 years by the Australian Bureau of Meteorology. (After Webb, Manolis and Buckworth 1983)

<table>
<thead>
<tr>
<th>Month</th>
<th>Temperature (°C)</th>
<th>Relative Humidity (%)</th>
<th>Rainfall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Daily max.</td>
<td>Daily min.</td>
<td>9 a.m.</td>
</tr>
<tr>
<td>Jan.</td>
<td>32.8</td>
<td>23.9</td>
<td>27.6</td>
</tr>
<tr>
<td>Feb.</td>
<td>31.7</td>
<td>23.9</td>
<td>26.8</td>
</tr>
<tr>
<td>Mar.</td>
<td>31.9</td>
<td>23.7</td>
<td>27.0</td>
</tr>
<tr>
<td>Apr.</td>
<td>33.0</td>
<td>22.1</td>
<td>26.8</td>
</tr>
<tr>
<td>May</td>
<td>32.0</td>
<td>19.4</td>
<td>24.8</td>
</tr>
<tr>
<td>June</td>
<td>31.1</td>
<td>17.0</td>
<td>22.8</td>
</tr>
<tr>
<td>July</td>
<td>30.9</td>
<td>15.1</td>
<td>21.5</td>
</tr>
<tr>
<td>Aug.</td>
<td>33.0</td>
<td>17.7</td>
<td>24.3</td>
</tr>
<tr>
<td>Sept.</td>
<td>34.7</td>
<td>20.3</td>
<td>26.9</td>
</tr>
<tr>
<td>Oct.</td>
<td>35.5</td>
<td>22.9</td>
<td>28.5</td>
</tr>
<tr>
<td>Nov.</td>
<td>35.5</td>
<td>23.8</td>
<td>29.1</td>
</tr>
<tr>
<td>Dec.</td>
<td>33.7</td>
<td>23.9</td>
<td>28.2</td>
</tr>
</tbody>
</table>
Table 2.2. Basic parameters relating to the seven major study sites

<table>
<thead>
<tr>
<th>Pool number</th>
<th>Maximum length (m)</th>
<th>Maximum width (m)</th>
<th>Maximum depth (m)</th>
<th>Crocodile population</th>
<th>Number of nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>320</td>
<td>40</td>
<td>4.2</td>
<td>45</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>235</td>
<td>100</td>
<td>3.2</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>315</td>
<td>80</td>
<td>1.8</td>
<td>48</td>
<td>29</td>
</tr>
<tr>
<td>4</td>
<td>735</td>
<td>60</td>
<td>2.5</td>
<td>28</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>85</td>
<td>20</td>
<td>2.7</td>
<td>74</td>
<td>7</td>
</tr>
<tr>
<td>6</td>
<td>150</td>
<td>40</td>
<td>2.0</td>
<td>15</td>
<td>2</td>
</tr>
<tr>
<td>7</td>
<td>800</td>
<td>100</td>
<td>&gt;3</td>
<td>8+</td>
<td>1</td>
</tr>
</tbody>
</table>

1 As at August 1983.
2 As captured in October 1983.
3 Number located in 1982 (Webb et al. unpublished).
+ Estimated from spotlight survey study 1983.
Fig. 2.1. The distribution of *C. johnstoni*. After Cogger (1979)
Fig. 2.2. The study area of Webb and coworkers. Major sites for this study are numbered. After Webb, Manolis and Buckworth 1983
Fig. 2.3. A view of Site Two from the air. Photo G. Webb.

Fig. 2.4. A view of a section of Site Four from the air. Photo G. Webb.
Fig. 2.5. The estimated age structure of the McKinlay River *C. johnstoni* population in 1979. After Webb, Buckworth and Manolis (1983a), Webb and Smith (1984) and Smith and Webb (1985).
Age in years (year of hatch)

Numbers of individuals

- Males
- Females

<table>
<thead>
<tr>
<th>Age in years (year of hatch)</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>5(74)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10(69)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15(64)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20(59)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>25(54)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>30(49)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>35(44)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>40(39)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER 3

METHODS

3.1 THE LOCATING OF NESTS AND THE MEASUREMENT OF BASIC PARAMETERS

Nesting areas at the major Sites had been identified by earlier studies (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984). From the first week of August until the end of the nesting period (defined by the cessation of digging), these areas were checked daily for signs of the digging that indicates crocodile activity. Additional areas around the major Sites were also examined opportunistically during this period.

Nests were located by probing the substrate with a stainless steel rod 0.3 cm in diameter and approximately 60 cm in length (Blake 1974; Webb, Buckworth and Manolis 1983d; Webb and Smith 1984). When located, the nest was partially excavated and the depth to the uppermost surface of the uppermost egg was measured. A temperature was recorded from near the centre of the clutch with a calibrated mercury thermometer. One to three eggs were removed from the nest and were weighed and measured. Any eggs found at that stage to have been pierced or severely dented by the probe (probed) were discarded. Substrate type, the height of the nest above water, and the horizontal distance of the nest from water were estimated at that time. Temperature probes were fitted to some of the nests, usually when first located.
Substrate type was classified by eye into one of seven categories: 1, fine sand; 2, medium/fine sand; 3, medium sand; 4, medium/coarse sand; 5, coarse sand; 6, sand/humus; and 7, sand/clay. Nest height above water was estimated by eye and the distance of the nest from the water’s edge was either estimated by eye or paced out. In the case of Site Three, which produced approximately 50% of all nests considered in this study, a detailed topographic map was prepared of the nesting area for each year from 1982 to 1985 and the information on that map was used to estimate the above parameters.

Each nest was covered with a square of wire netting (50 x 50 cm) which was pegged to the substrate in an attempt to restrict access to the eggs by predators (Webb and Smith 1984). Also, the substrate around the nest was sprayed with room deodoriser to mask the smells of both the turned soil and the mucus on the eggs, which could attract predators.

3.2 THE ESTIMATION OF LAYING DATE

When a clutch was discovered, the condition of the uppermost eggs (1-3) was examined. If an opaque band was present, its extent around the egg was estimated to the nearest 1/10 of the egg circumference and its maximum width was measured. If the opaque band encircled the egg completely, its maximum and minimum widths were measured. The amount of mucus on the eggs was classed as none, little, moderate or abundant.
When eggs had no opaque band and had abundant mucous, the clutch was considered to have been laid the previous night and was accorded the day before discovery as the day of laying. Clutches with less than abundant mucous, and no opaque band, were considered possibly infertile but not necessarily laid the previous night. Therefore, they were not accorded a definite day of laying and hence play a limited role in the analyses that follow. Clutches that were found to have an opaque band that did not entirely encircle the egg were considered to be aged as follows: 1 day, spot or 1/10 complete; 2 days, 2/10 - 5/10 complete; 3 days, 6/10 to just complete. This scheme is drawn from the data of Webb, Buckworth and Manolis (1983d), Webb, Buckworth, Sack and Manolis (1983), Webb, Beal, Manolis and Dempsey (1987), Webb, Manolis, Dempsey and Whitehead (1987), and Webb, Manolis, Whitehead and Dempsey (1987). Those clutches in which the opaque band completely encircled the eggs could not be accorded an age and hence play a limited role in the analyses that follow. The exclusion of clutches on the basis of lack of laying date accounted for few nests, and then, only in some analyses.

3.3 THE RELOCATION OF NESTS

In 1983, five nests located in the upstream section of the study area were removed to a laboratory incubator in early November, just prior to the expected hatch date. This was done because access to those nests was likely to be prevented by early wet season rains. Additionally, one nest was removed from Site Three to the incubator as it was in immediate danger of having been washed away by early wet-season rains. The incubator used was not a constant temperature
environment, but had a mean temperature of 32.5°C with a range over the 19 days that it was used of 1.2°C, i.e. ± 0.6°C (range). The eggs were incubated over open water to maintain a high level of humidity.

In 1985, all nests located at Sites other than Site Three were relocated to Site Three, so that parameters of the nest environment that were highly correlated (e.g. egg size and nest depth; Chapter 4) could be artificially manipulated. For relocation, the eggs were numbered and had a cross marked on their uppermost point before being removed from the nest. This marking allowed the eggs to be repositioned at their original orientation in the artificial nest (Joanen and McNease 1981a; Webb, Buckworth and Manolis 1983d). The eggs were packed in nest substrate (usually sand) inside on a styrofoam container. At Site Three, the artificial nests were made in an area adjacent to that actually being used for nesting by Site Three females. The eggs were buried within the normal range of nest depths except that clutches of large eggs were generally buried shallower than clutches of small eggs.

Where nests that completed their development in an incubator have been used in analyses, their observed incubation times have been used; no adjustment has been made for possible effects of the changed temperature regime during the final stages of incubation. Webb, Beal, Manolis and Dempsey (1987) found that changes in temperature during late incubation have little influence on total incubation time, as the rate of embryonic development appears to be determined by temperatures experienced early in incubation. Accordingly, errors arising from this procedure are likely to be small (1-2 days).
3.4 NEST EXCAVATION AND THE MAPPING OF NESTS

At the time when hatching was expected to begin (around the last week of October; Webb, Buckworth and Manolis (1983d)], each nest was visited daily and the substrate above it struck by hand. This caused the hatchlings to begin calling if they were at the point of hatching. If so, the nest was opened, a temperature was recorded from near the centre of the clutch, and the position of eggs within the nest then mapped (Ferguson and Joanen 1982, 1983; Webb and Smith 1984). This process involved recording, for each egg, its position relative to other eggs in the nest, the egg's depth, and angle of its major axis to the horizontal. Each egg was removed from the nest, and measured if possible - some were in the process of hatching when excavated, and thus could not be measured. The egg dimensions measured were used to estimate egg weight at laying from formulae provided by Webb, Buckworth and Manolis (1983d).

Within 12 hours of hatching, all animals were weighed, measured and sexed. In 1983, animals were sexed by examination of the gonad, and the residual yolk was weighed. In 1984 and 1985, sex was generally determined by examination of the cliteropenis (Webb, Manolis and Sack 1984) and residual yolk weight was predicted from abdomen dimensions as described by Smith and Webb (1987; Appendix 2). Where any doubt existed about the sex of an animal as indicated by cliteropenis morphology, the animal was sacrificed: gonad morphology was used to determine sex, and residual yolk weighed.
Where a nest had not hatched within a week of its expected hatch date, it was opened and mapped. All such nests did not contain viable embryos.

In the analyses that follow, day of laying and day of hatching are treated as consecutive numbered days relative to July 31 each year: day 1 was August 1. Day of hatching is treated as the day on which the nest was mapped, as the nest would probably have been excavated that night (Chapter 5).

In situations where a crocodile had partly or completely excavated a nest, such data as were available were collected. Attempts were made to capture any hatchlings at liberty. If recaptured hatchlings could unequivocally be assigned to a particular nest, they were included in the analysis on that basis: otherwise they were excluded.

### 3.5 CLASSIFICATION OF EGGS AND EMBRYOS

All eggs and embryos examined in this study were classified into one of nine categories. They were:

1. Eggs which showed no signs of development;
2. Eggs which had suffered major laying dents and did not initiate or complete development;
3. Eggs which had been probed;
4. Eggs in which embryos died for no apparent cause;
5. Eggs in which embryos were drowned in the nest by rising water levels;
6. Eggs with embryos that died in the process of hatching, or soon after;

7. Eggs which were hatched by an adult, and the subsequent fate of the hatchling was unknown;

8. Eggs which hatched and which produced hatchlings which appeared normal (see below);

9. Eggs which hatched and which produced hatchlings which appeared abnormal (see below).

Abnormalities of embryos and hatchlings of *A. mississippiensis* have been catalogued by Ferguson (1985), and those of *C. porosus* by Webb, Sack, Buckworth and Manolis (1983). The most common evidence of abnormality include a kinked tail or spine, a pronounced 'bump' on the cranial platform, and a distended or shorted abdomen.

3.6 STATISTICAL ANALYSES

"INSUFFICIENT UNITS WITH POSITIVE WEIGHTS ARE NON-MISSING"

(Genstat error message)

Comparison of samples in this thesis relies primarily on F-tests, t-tests appropriate to the equality or inequality of variances, ANOVA, and \( \chi^2 \) for 2x2 contingency tables (Sokal and Rohlf 1969). Generalized linear models, of which regression analysis is a simple form, are also used extensively (GENSTAT; Alvey et al. 1982; Dobson 1983; McCullagh and Nelder 1983). In assessing the overall goodness of fit of generalized linear models, where possible, percentage of
variance explained is usually used. While a coefficient of determination ($r^2$) may be calculated, percentage of variance explained is more appropriate as a comparative measure.

In the analysis of hatchling survival, a form of logistic regression analysis (a generalized linear model) is used. The dependent variable is binary, with survival coded as one and non-survival coded as zero. The method uses maximum likelihood estimators and thus variance is replaced with deviance as the measure of variation. The distribution of errors is not assumed to be normal, as is the case with multiple regression, but rather is assumed to be binomial. The change in total deviance attributable to fitting an explanatory variable to the model is equivalent to a $\chi^2$ statistic. Given that the expected frequency for any one observation in the model should never be greater than one, it is impossible to construct a goodness of fit statistic for the model as a whole (Dobson 1983). The model predicts a probability between zero and one. Consequently, when examining the power of the model, individuals with a predicted probability of less than or equal to 0.499 are considered as zero, while those with a predicted probability of greater than 0.499 are considered as one. These allocations to survivor or non-survivor can then be compared to the observed data.

The analysis of embryonic survival and sex determination employs a different form of logistic regression. In this case, the analysis considers the proportion of either survivors or males respectively resulting from each clutch. Binomial variance is again assumed, but because the sample size related to each observation is
generally greater than one, a goodness of fit statistic can be derived for the model as a whole. The distribution of the residual deviance of the model is asymptotic to a $\chi^2$ distribution and thus the residual deviance may be compared to a $\chi^2$ distribution to determine if the model is a good fit.

In most of the regression analyses, nominal classifications (factors) are used as explanatory variables. These may be non-continuous characters such as sex, but they can also be derived from continuous variables such as head length. By converting a continuous variable to a nominal variable, i.e. treating it as factor, it is possible to observe it over its range to determine whether it displays non-linearity of any form. Moreover, by treating continuous variables as factors, they are not constrained to linearity or any form of transformation, but rather simply reflect their true relationship to the dependent variable. All explanatory variables were available for modelling as factors. Each variable was ranked from the highest value it took to the lowest. This progression was then divided into up to 10 equally sized groups, or groups as nearly as equal in size as was possible. For example, in the case of 10 groups, the lowest 10% of head length measurements would form one group, the next lowest 10% another group and so on.

This process served to reduce head length from a continuous variable with many different values to a nominal classification of only 10 classes. The value of each of those classes (levels) was the mean of that 10% of the total sample that fell in that class. One particular benefit of this technique is that no matter what form of
relationship exists between the explanatory factor and dependent variable, no transformations are required, and all explanatory factors account for the same number of degrees of freedom in the model. Thus, the change in total deviance (or variance) attributable to various explanatory factors is directly comparable as a $\chi^2$ (or $F$) statistic with the same degrees of freedom. When continuous variables are transformed into factors of ten levels, the change of deviance attributable to them can be compared to the distribution of $\chi^2_{9}$ (or $F_{9,n}$): a factor thus always accounts for degrees of freedom that are one less than the number of levels of the factor.

When the model evaluates the contribution of a factor, the effect of each of the levels of that factor is assessed relative to the effect of the lowest level of the factor, which has its coefficient arbitrarily set to zero. The effect of each level of the factor is assumed to be independent and additive, and thus the coefficient attributable to a factor level is additive in the predictive equation generated.

This technique of transforming continuous variables to factors does result in some loss of information in analyses. Their use can, however, be justified on a number of grounds. First and foremost, the relationships displayed by explanatory and dependent variables are rarely simply linear and for that reason cannot be adequately modelled by simple or complex transformations. The attempt to model such relationships using continuous variables, no matter how transformed, leads to a considerable loss of information by constraining the data to a relationship they do not fit.
Secondly, generating a model where, say, one variable is included as two transforms and another included as three transforms makes the true contribution of each of those variables difficult to establish and even more difficult to compare. Thus, the use of factors is justified in that they simply describe a relationship rather than force it to some prescribed transformation, and so allow different variables to be compared directly.

Significant interaction terms may exist between modelled factors. Such interactions are difficult to interpret in biological terms and become unwieldy in statistical terms. Therefore, depending on the complexity of the existing model, they have on occasion been ignored. At the completion of the modelling process, predictions can be formed along with approximate standard errors, and these are used to provide a graphical or tabular representation of the relationship between the explanatory and dependent variables.

The use of predictive formulae generated by generalized linear models which include a combination of simple variables, factors and interaction terms can be complex. An example of a fictitious simple model is given below. The principles of interpretation of this model apply equally to larger, more complex models of the kind to be encountered in later sections of this thesis.

The model is:

\[ \text{Footsize} = 0.13 \times \text{Height} + \text{Sex} + \text{Sex.Height} \]
where Sex is a two level factor with level one being male and level two being female. As male is the lower level of the factor, its coefficient for both the main effect (Sex) and interaction (Sex.Height) terms is set to zero. Thus the predictive equation for male is:

Footsize = 0.13 x Height.

The result for female is more complex with the fictitious coefficients for the main effect (Sex) and interaction (Sex.Height) being -0.03 and -0.01 respectively. When these coefficients are introduced into the model,

Footsize = 0.13 x Height - 0.03 - 0.01 x Height

which becomes -

Footsize = 0.12 x Height - 0.03.

From the above it can be seen that a unique predictive formula is derived for each level of the factor. The simple interpretation of a main effect is that it modifies the value of the model's intercept, whereas the interaction term between a factor and a simple variable modifies the slope associated with the simple variable. Interaction terms between factors modify only the intercept, as there is no slope associated with a factor.
In the Chapters that follows, a number of generalized linear model formulae are presented. The coefficients for main effect and interaction terms are tabulated for ease of reference. Where an explanatory variable occurs as both a simple variable and in an interaction term, the coefficient presented for the simple variable is in fact the value of the lowest level of the interaction term.

In a generalized linear model, one or more levels of a factor may be missing in a main effect and/or interaction term. Such levels are referred to as aliased. Aliasing may commonly arise in two ways, designated as extrinsic and intrinsic. Extrinsic aliasing occurs when a particular level of a factor does not appear in a data set. For example, when fitting substrate type as a seven level factor, to a subset of data, there may be no nests from coarse sand (level five of the factor, see Section 3.1) in the sample. Thus, level five of the factor is aliased.

Intrinsic aliasing occurs through attempting to fit a term to a model which is linearly dependent on one or more terms already in the model. Intrinsic aliasing may occur with both simple variables and factors. If, in the case of a simple variable, two terms are in the model and an attempt is made to fit the mean of those terms as a third term, the attempt will fail as the third term can be described by the first two terms. The situation with factors is similar. Consider the case of two factors: a three level factor of year relating to 1983, 1984 and 1985; and a factor where each level is a different nest. In a model, it is possible to fit year and remove the average difference between the three years, and then to fit nest and account for any
existing variation between individual nests. The reverse procedure cannot be done. If nest is fitted first, the variation between individual nests also includes the general difference between years. Thus, when an attempt is made to fit year, it is aliased because it contains no information that was not already accounted for by fitting nest.

The development of the statistical models presented in the Chapters that follow was not without difficulties. These stemmed primarily from two sources. First, since the data were derived from field studies, in many cases all explanatory variables were not available for each observation. The inclusion of an additional explanatory variable in a model necessarily changed the size of the sample available for modelling and made the comparison of models containing different explanatory variables difficult. Two possible remedies for this problem, namely pair-wise deletion of missing data and the use of multivariate correlation analysis to estimate missing data, were dismissed on the grounds of the statistical difficulties of the former, and the circularity inherent in the latter.

The second source of difficulty was the existence of correlations between many of the available explanatory variables. These correlations often rendered models unstable, thus requiring the removal of some of the explanatory variables. The choice of which variables to remove was, by necessity, based on both statistical and biological grounds.
While the models presented in the following Chapters are certainly not the only possible statistical descriptions of the data, they are considered to provide the most biologically meaningful and statistically sound description. They are, therefore, to an extent subjective, and must be viewed as such. No attempt will be made to present the many hundred alternative models which were explored and rejected.
4.1 INTRODUCTION

The dynamics of the nesting season of *C. johnstoni* in terms of timing, duration and changes in clutch parameters, has been described in general terms (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984; Chapter 2). However, these attributes of the nesting season are subject to variation, and the causes of such variation have received only cursory examination to date. This is largely due to the fact that an intensive study over a relatively long period is required to gain the needed insights into those processes.

Not only does the timing of nesting vary between years, but nesting effort too appears to vary between years. The causes of the variation are currently unknown, though extensive data for Alligator *mississippiensis* suggest that weather patterns are the major determinants of the time of nesting in this species (Joanen 1969; Joanen and McNease 1979, 1981b; Dietz and Hines 1980; Wilkinson 1983).

Webb and Smith (1984) identified differential survival effects related to laying date within the nesting season. However, their results relate to a single season and so their general applicability remains to be established.
In this Chapter, nesting in *C. johnstoni* is examined, paying particular attention to nest site selection and changes in clutch parameters within and between nesting seasons. Webb, Buckworth and Manolis (1983d) have shown that larger females tend to lay larger clutches of larger eggs earlier in the nesting season (Webb, Buckworth and Manolis 1983d). It has also been shown that the sex and survival of *C. johnstoni* embryos is related to the time of laying (Webb and Smith 1984). These two results therefore beg the question: is there a relationship between the size (age) of a breeding female and the sex and probability of survival of her offspring?

Much of the analysis in this Chapter relies on the simulation model developed for this population by Smith and Webb (1985). Not only are published parameters and predictions of the model used, but the model itself is employed to estimate new parameters. As such, the model plays an integral role in this Chapter, and the published account of the model (Smith and Webb 1985) appears as Appendix 3.

### 4.2 RESULTS

#### 4.2.1 RELATIONSHIPS BETWEEN FEMALE SIZE AND CLUTCH PARAMETERS

Unpublished data are available on the clutch parameters (mean egg weight, clutch size, total clutch mass) of eight female *C. johnstoni* of known size (Table 4.1). Complete data were available for six of the females, with one female having only a known size and a known clutch size, and a second female having only a known size and known clutch mass (Table 4.1). Three of the animals were from the
McKinlay River population (Webb, Buckworth and Manolis 1983d and unpublished), two were from the Katherine River (H. Cooper-Preston unpublished) and two were initially from the Mann River but were subsequently maintained at Melbourne Zoo (C. Banks pers. comm. to G. Webb). The clutch parameters were modelled against log_{10} snout-vent length (SVL) as this provided a better fit than did SVL or ln SVL.

The three relationships established (see Section 3.6 and Fig. 4.1) were:

Mean Egg Weight = -87.2644 + 81.5451 \times \log_{10} SVL \quad \text{Eq. 4.1}

(F_{1,4} = 18.58, 0.025 > P > 0.01)

Clutch Size = -80.3763 + 47.7753 \times \log_{10} SVL \quad \text{Eq. 4.2}

(F_{1,5} = 55.74, 0.001 > P)

Clutch Mass = -5647.7916 + 3330.3508 \times \log_{10} SVL \quad \text{Eq. 4.3}

(F_{1,5} = 59.38, 0.001 > P).

The relationship between clutch mass and log_{10} SVL is slightly stronger than that between clutch size and log_{10} SVL. The relationship between egg weight and log_{10} SVL is the weakest of the three.
4.2.2  NEST SITES AND THEIR SELECTION

4.2.2.1  GENERAL

The nature of the nest sites utilized by *C. johnstoni* has been described previously (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984; Whitehead 1987a; Chapter 2). By way of generalisation, it can be said that females of *C. johnstoni* appear to nest in any available friable substrate, especially close to water.

The nesting banks utilized by *C. johnstoni* at the major study Sites in the M'Kinlay River area are varied but, consistently, the actual sites chosen on the banks involve patches of bare sand. They range from a location at Site 1 (Fig 4.2) where only one female nested, and which was adjacent to the pool and had a substrate combination of loosely packed leaf litter and sand, to the colonial nesting bank at Site 5 which is approximately 40 m from the pool and involved a large area of apparently homogeneous coarse sand in the M'Kinlay River mainstream. Small, low-lying sand banks, like the examples from Sites 1 and 4 (Figs. 4.3, 4.4 and 4.5), were the most commonly utilized type of nesting bank. The only known nesting location at Site 7 (Fig. 4.6) was initially lightly vegetated with annual grasses each year. Here the crocodiles remove the dead grass, and leaving a substrate of medium and fine sands.

Major colonial nesting areas occurred at Sites 3 and 5. At Site 5, nesting occurred in the M'Kinlay River mainstream, adjacent to the pool. At nesting, the mainstream consists of large expanses of
sand broken by occasional pools. At Site 5, nesting occurred in the areas shown in Figs. 4.7 and 4.8. From observation, the only distinguishing feature of the area chosen by *C. johnstoni* for nesting at Site 5, by comparison with the adjacent areas of river bed, was its proximity to the pool in which the crocodiles spent their time. During the 1984/85 wet season, a bank of fine sand (Fig. 4.9) was deposited adjacent to the usual nesting areas associated with Site 5, though it was further from the pool. As judged by the extent of digging, the pool was the subject of much investigation by *C. johnstoni*. Only one nest was laid there and it consisted of seven small eggs, none of which underwent development. A large section of the bank, including that which contained the nest, was washed away by early wet season rains.

Site 3 was perhaps the most important nesting site. It was colonial, and more than 15 nests were found there in each of the years it was examined. Those examinations over a period of time have provided a useful view of the nesting bank. Photographs taken in 1978, 1979, 1983 and 1985 (Figs. 4.10, 4.11, 4.12 and 4.13) clearly show that the nesting bank has become progressively more vegetated over this period. Areas previously used for nesting were completely overgrown by 1985, thus restricting the potential choice of nest sites. An even more marked example of the vegetating of nesting banks is shown in photographs taken in 1979 and 1985 of a nesting bank at a pool in the upstream area in the McKinlay River (Figs. 4.14 and 4.15).

The structure of the nesting bank at Site 3 has been changing, as was evident from the topographic maps prepared annually
for the period 1982-85 and is clearly seen by reference to Figs. 4.10-4.13. As a result of the deposition of additional sand during the wet season, the bank has increased in size and moved further into the pool. When the locations of nests are marked on topographic maps it is evident that the distribution of nests is not random.

4.2.2.2 METHODS

Data were collected from Sites 3 and 5 in an attempt to elucidate the nest site selection process inferred from the non-random distribution of nests at those Sites. Fifty two points were randomly selected on the nesting bank at Site 3 and ten were randomly selected in a 5 x 14 m area of sand bank in the mainstream at Site 5 where nesting was expected to occur. At each of these data points, the following variables were measured: substrate type; friability; hours of direct sunlight per day; whether the point was overhung with vegetation and if so at what height; the substrate temperature at 18.00 hours at 20 cm below the surface; the distance from water; the distance from the nearest tree; the presence or absence of grass; the height above water; and, whether females had already been digging at that point. Friability was estimated by applying a 5 kg downward pressure to a nest probe (Chapter 3) and recording the number of centimetres by which the probe penetrated the substrate. This measure was repeated three times at each point and the average was used in analyses. All data were collected over a 12 hour period on the same day, 11 August 1984.
After nesting was completed, the location of nests was overlayed on maps showing the points at which data had been collected. From those maps, the dependent variable was estimated in terms of those data points which had a nest laid within 2 m of them. This variable was coded as binary, with the presence of a nest indicated by one and the absence by zero. Radii smaller than 2 m generated a dependent variable with too few positive responses, and radii greater than 2 m generated a dependent which could not be adequately modelled.

In exploring the behaviour of the dependent variable (Section 3.6), the explanatory variables of friability, hours of direct sunlight, temperature, distance from water, distance from the nearest tree and height above water were converted to three-level factors. Substrate type was coded as a three-level factor in order to be comparable to the above variables: the three levels of the factor were equivalent to fine, medium and coarse substrates. Logistic regression was employed in the analysis of these data, with the fitted value representing the probability of a nest being laid within 2 m of a data point.

The three-level factors were estimated separately for Sites 3 and 5 using the method detailed in Section 3.6. The data from Sites 3 and 5 were modelled separately as Site 5 was far less variable than Site 3. All data points at Site 5 had a uniform substrate, were exposed to the same number of hours of direct sunlight per day, were under an effectively unbroken canopy of greater than 10 m height, and had no grass. Therefore, the suite of explanatory variables at Site 5 was much reduced.
4.2.2.3 RESULTS

The most important explanatory variable at Site 3 was the presence or absence of grass \( (X^2_1 = 6.7930; 0.025 > P > 0.01) \). The next most important variable was the three-level factor of temperature. The behaviour of temperature was extensively explored and was found to be best described by a two-level factor distinguishing those sites with a temperature less than 30°C from those with a temperature greater than, or equal to, 30°C \( (X^2_1 = 7.2192; 0.01 > P > 0.005) \).

Of the 14 data points associated with nests, 11 (79%) were correctly identified by the above statistical model. An additional nine data points were identified as probable nesting sites. Thus, of the 52 data points examined, 20 (38%) were predicted to be suitable for nesting. The predicted probability of nesting within 2 m of data points categorised by the presence/absence of grass and by temperature appears in Table 4.2.

Whether or not a female had previously been digging at a point was also significant in the analysis [as data were collected on 11 August, digging occurred subsequently at many sites as the nesting season progressed]. When this variable was included in the analysis the resulting model correctly predicted 10 of the 14 (71%) of nesting sites, and therefore was somewhat less accurate. At the mean values for the presence of grass and for temperature, the model predicted that 37% of points where females dug would be nest sites. Thus, the observation that a female digs at a point does not necessarily mean that she will nest there: a result concordant with extensive observation.
In an attempt to predict where a female would dig, the model was restructured in such a way that whether or not a female had dug at a point became the dependent variable. Two explanatory variables were significantly related to whether or not a female dug at a site. They were the presence of grass ($\chi^2_1 = 5.203; 0.025 > P > 0.01$), and temperature as a two level factor ($\chi^2_1 = 4.801; 0.05 > P > 0.025$).

Thus, the absence of grass and a high enough temperature induce a female to dig at a point, and these two factors subsequently determine if she will nest there. This contention was investigated with a sequential two stage model. The first stage was used to predict which of the data points was suitable for digging. The behaviour of temperature in this first stage was re-examined. It was found to be best described by a two level factor, distinguishing those sites with a temperature of at least 28.0°C from those with a lower temperature.

The model identified 28 points suitable for digging and these included 12 of the 14 subsequent nest sites, and excluded all grassed sites.

When these 28 sites were analysed as the second stage of the model, temperature was the only variable significantly associated with nesting. The behaviour of temperature was best described by a two-level factor identifying those sites with a temperature of at least 30°C from those with a lower temperature. The second stage of this model correctly identified 11 of the 12 nest sites which the previous model had identified as points at which digging would occur. The model also identified a total of 20 points as probable nesting sites.

The first stage of this model predicted that digging would occur at sites without grass and with a temperature not less than
28°C. The second stage of this model predicted that of such sites, those with a temperature not less than 30°C were probable nesting sites.

The one and two stage models were equivalent in that they both correctly identified the same 11 of 14 nest sites, and predicted that a total of 20 points were acceptable nesting sites. They differed in that the two stage model provides greater insight into the nest site selection process.

The temperature model derived in Section 5.2.2 for a series of C. johnstoni nests was used to predict the nest temperature at 18.00 hours on the day of laying. The mean predicted temperature was 29.96°C. Of the 49 nests for which the temperature model was derived, 25 had a temperature greater than or equal to 30.0°C and 42 of 49 had a temperature of greater than or equal to 28.0°C. These results indicate a slight discrepancy between this analysis of nest site selection and the predictions of the model of nest temperature derived in Section 5.2.2. However, while temperatures were recorded for the analysis nest site selection at a depth of 20 cm, the temperatures used to develop the model of nest temperature were recorded at a shallower depth.

The analysis of the ten data points at Site 5 failed to demonstrate a significant association between any of the available variables and nest site selection. Possible reasons for this will be discussed later in this Chapter.
4.2.3 TIME OF NESTING

Accurate dates of laying were available for 146 nests. These were located in the downstream section of the McKinlay River both during 1980 and the period 1982-85. Data for 1980 are from Webb, Buckworth and Manolis (1983d) while those for 1982 are from Webb and Smith (1984 and unpublished).

The distribution of the day of laying for each of these five years is shown in Fig. 4.16. The mean and median day of laying for each of those years appears in Table 4.3. The mean day of laying is not a particularly sound measure as the distribution of laying day does not appear to be normal, especially in 1982 and 1983 (Fig. 4.16). There is marked variation in the time of laying among years. For example, in 1983 laying occurred between days 25 and 44, whereas in 1984 laying occurred between days 10 and 34. However, the distribution of laying date in each year overlaps the distribution of laying date in every other year.

From studies of the nesting ecology of Alligator mississippiensis, it is known that ambient temperature in the three months preceding nesting can influence the day of laying (Joanen 1969; Joanen and McNease 1979, 1981b; Wilkinson 1983). Therefore, the median days of laying for the five years considered were examined against temperatures from the preceding four months. The temperatures used were the means of the daily maxima and of the daily minima for each of the months. The temperatures were recorded at Middle Point, 50 km northeast of the study area. The months considered were April-July inclusive.
Of the eight regressions, only one was significant, and that was median day of laying versus the mean of May maximum temperatures, as given by the equation:

\[
\text{Median day of laying} = 270.16 - 7.57 \times \text{Mean May Max.} \quad \text{Eq. 4.4}
\]

\[(F_{1,3} = 13.24; \ 0.05 > P > 0.025; \text{Fig. 4.17}).\]

Over the period 1965-85, the mean of May maximum temperatures varied between 30.0 and 33.9 with an average of 32.3°C. These three temperatures predict median days of laying of 43.1 (12 September), 13.5 (13 August) and 25.6 (26 August) respectively. The precise relationship between temperature and median laying date is probably not linear, but the data available are insufficient to detect any non-linearity.

Rainfall is unlikely to be a major influence on time of nesting in C. johnstoni. However, it may be an influence on nesting effort. Little rain falls in the three months preceding nesting. For the period 1957-1985, rain fell at Middle Point on an average of two days in May, and on no days in June, July or August. In the five years considered here, no relationship between rainfall patterns and median day of laying could be discerned.

The time within a nesting season at which a female C. johnstoni lays is related to her size (Webb, Buckworth and Manolis 1983d), as it is in Caiman crocodilus (Staton and Dixon 1977) and A. mississippiensis (Ferguson 1985). The McKinlay River C. johnstoni population is recovering from a period of intensive hunting in the
early 1960’s and the age and size structures of the population are still unstable (Webb and Smith 1984; Smith and Webb 1985). The simulation model of the population developed by Smith and Webb (1985; Appendix 3) predicts changes in the age and size structures over the period under study. The predictions of the model have previously been found to be consistent with observed changes in the population (Smith and Webb 1985).

Given that the time of nesting is related to the size of the female and that the size and age structures of the population are changing, then some of the annual variation in median day of laying could be attributable to changes in the age and size structures. The population simulation model (Appendix 3) was therefore used to predict the mean age of females between 9 and 45 years of age that were expected to breed in each of the five years. The sizes of the females was estimated using the relationship between mean egg weight and female size (Section 4.2.1). Neither mean size nor mean age (Table 4.4) was significantly related to median day of laying ($F_{1,3} = 0.21$ and $F_{1,3} = 0.27$ respectively).

4.2.4 VARIATION IN CLUTCH CHARACTERISTICS WITH RESPECT TO DAY OF LAYING

Webb, Buckworth and Manolis (1983d) found that for a sample of 55 *C. johnstoni* clutches from the McKinlay River area collected in 1980, total clutch mass, clutch size and mean egg weight decreased significantly with day of laying. Twenty nine of those clutches were from the downstream area and so were available for analysis. With
similar data for 77 clutches from 1982-1985, these were used to re-examine the trends. One available clutch was not used in the analysis of clutch size and clutch mass as it contained only one egg, thus being atypical.

Total clutch mass was estimated in 1980 by weighing most or all of the eggs in the clutch. In 1982-85, the dimensions of a sample of eggs from each clutch was used to estimate mean egg width and length and these in turn were used to estimate mean egg weight using the formula provided by Webb, Buckworth and Manolis (1983d). The mean egg weight was then multiplied by clutch size to estimate total clutch mass. The proportion of a clutch used to estimate total clutch mass varied widely. Therefore, it was necessary to weight the analysis because confidence in the estimated total clutch mass and mean egg weight varied. The weight used took into account both the proportion of the clutch measured and the number of eggs measured and assumed equality of variance among clutches (Snedecor and Cochran 1980; Draper and Smith 1981). This assumption is supported by those clutches where most or all eggs were measured.

When each of the years was considered separately, day of laying was not found to be significantly related to estimated total clutch mass (Fig. 4.18). However, when all years were pooled, day of laying accounted for 7.3% of the total variance in accordance with the equation:

\[
\text{Total clutch mass} = 1164.00 - 13.36 \times \text{Day}
\]

\(F_{1,104} = 9.24; \ 0.005 > P > 0.001; \ \text{Fig. 4.19}).\)
This formulation does not take into account the variation in median day of laying with respect to year (Section 4.2.3). Therefore, day of laying was recalculated for each year in four ways: first, relative to the day of laying of the first nest of the season; second, relative to the day of laying of the final nest of the season; third, as the deviation between that day of laying and the mean day of laying for that year; and fourth, as a percentage of the nesting season completed when the nest was laid. With respect to changes in total clutch mass, none of these measures accounted for more of the variance in the pooled data than day itself. Respectively, they accounted for 4.3, 5.2, 3.9 and 5.9% of the variance.

Clutch size was analysed using an unweighted regression as both clutch size and day of laying were precisely known. Clutch size was not found to vary significantly with respect to day of laying when each year was treated separately (Fig. 4.20). When the data were pooled, day of laying accounted for 9.5% of the variance with:

\[
\text{Clutch size} = 16.05 - 0.1572 \times \text{Day} \quad \text{Eq. 4.6}
\]

\((F_{1,105} = 10.73; \: 0.001 > P; \: \text{Fig. 4.21})\).

The four transformed expressions of day of laying were less useful descriptors of the change in clutch size, accounting for 6.5, 6.2, 6.1 and 7.1% of the variance respectively.

As samples of eggs were used to estimate the mean egg weight for the clutch, mean egg weight was analysed using weighted regression. The clutch of one egg was included in the analysis, as
clutch size and clutch mass, but not egg size, was atypical. The distribution of mean egg weight with respect to day of laying was similar to that for estimated total clutch mass and clutch size with respect to day of laying. Day of laying was not significant with respect to mean egg weight when each year was treated separately (Fig. 4.22). The pooled data, however, behaved differently. Mean egg weight was most significantly related to day when treated as the percentage of the nesting season completed (P Day; Fig. 4.23), which accounted or 3.3% of the variance with:

Mean egg weight = 70.57 - 0.0596 x Pday

(F1,105 = 4.59; 0.05 > 0.025)

the untransformed day accounted for only 1.8% of the variance (Fig. 4.24).

The distribution of clutch parameters, with respect to day of laying, contains information about the size of the females which nest at particular times (Section 4.2.1). However, since there is evidence that clutch size and clutch mass may decline among particularly large or old females (Webb, Buckworth and Manolis 1983d; Ferguson 1985), the use of clutch size or clutch mass may underestimate the size of particularly old or large females. To investigate this possibility, the SVL's of the breeding females were predicted from clutch size 
(SVLcs), clutch mass (SVLcm) and mean egg weight (SVLewt), using the reverse formulae to those derived in Section 4.2.1 (Equations 4.1, 4.2 and 4.3). The differences between the sizes predicted from mean egg weight and those predicted from clutch size (SVLcs - SVLewt; Fig.
(4.25) and from clutch mass \((SVL_{cm} - SVL_{ewt}; \text{Fig. 4.26})\) supports the contention that larger females may display a reduction in clutch size and mass. To remove this source of variation, clutches which predicted an \(SVL_{ewt}\) greater than both \(SVL_{cs}\) and \(SVL_{cm}\) were excluded. The average of \(SVL_{ewt}', SVL_{cs}\) and \(SVL_{cm}\) (\(SVL_X\)) was calculated for each of the remaining clutches.

There appears to be a consistent difference between \(SVL_{cs}\) and \(SVL_{ewt}\) (Fig. 4.25). The cause of this is simply that within any clutch size, there tends to be an increase in egg weight until the next clutch size is reached. Thus, an apparently systematic bias results from the use of a quasi-continuous variable (clutch size) and a truly continuous one (egg weight) to estimate \(SVL\).

When all years were pooled, day of laying accounted for 4.2% of the variance in \(SVL_X\) (Fig. 4.27). The relationship was:

\[
SVL_X = 99.62 - 0.615 \times \text{Day}
\]

\((F_{1,71} = 4.12; 0.05 > P > 0.025).\)  

When modelled against the proportion of the nesting season completed (\(P_{day}; \text{Fig 4.28})\), the relationship was:

\[
SVL_X = 93.44 - 18.78 \times P_{day}
\]

\((F_{1,71} = 8.15; 0.01 > P > 0.005).\)

Thus, the proportion of the nesting season completed is a far better descriptor of female size than is the day of year on which nesting occurs.
The relationship between $SVL_X$ and $P$ day predicts that the first females to nest have an $SVL_X$ of 93.4 and that the last to nest have an $SVL_X$ of 74.7 cm. The average maximum $SVL$ of female $C. johnstoni$ in the downstream section of the McKinlay River is 95.5 cm and the average $SVL$ at maturity is 74 - 78 cm (Webb, Buckworth and Manolis 1983a, d).

4.2.5 VARIATION IN TOTAL NESTING EFFORT AND CLUTCH PARAMETERS AMONG YEARS

The estimate of total nesting effort used was simply the total number of nests located in each of the years. Total nesting effort was 40, 46, 35, 47 and 35 clutches respectively for the period 1980, 1982-85.

Clutch parameters also varied in this period. Frequency distributions of clutch size appear in Fig. 4.29 and 4.30. Clutch size varied from one to 20 and thus formed a frequency distribution of 20 size classes. In order to present the distributions of clutch mass and mean egg weight in a comparable form, they also are shown as frequency distributions of 20 equally broad size classes. These appear in Figs. 4.31 and 4.32 and those of mean egg weight appear in Figs. 4.33 and 4.34. Descriptive statistics of the distributions of clutch size, clutch mass and mean egg weight are given in Tables 4.5, 4.6 and 4.7 respectively.

While the frequency distributions do not in general appear normal from simple inspection, Tables 4.5-7 indicate that none of the
distributions is significantly skewed or kurtotic. Thus, there appears to be no statistically significant lack of normality.

Over the period under study, the three clutch parameters demonstrate slightly different profiles (Fig. 4.35). All increase from 1979 to 1980, and clutch mass is then relatively stable until it drops in 1985. Mean egg weight increases from 1979 to 1983 and then falls in both 1984 and 1985. Clutch size increases from 1979 to peak in 1980, drops in 1982, remaining constant in 1983 to drop in both 1984 and 1985.

It is not easy to interpret this variation in total nesting effort and clutch parameters. Among those females available to breed, only a proportion do so, and that proportion is related to the size and age of the female (Webb, Buckworth and Manolis 1983b, d; Smith and Webb 1985). It can also be expected to relate to weather patterns in some way (Wilkinson 1983). The relationship may vary with the size of the female: small females may, for example, be more sensitive to extreme temperatures than are large females (Wilkinson 1983). Finally, the age and size structures of the McKinlay River C. johnstoni population changed during the course of this study (Smith and Webb 1985) and the changes can be expected to be reflected to some extent in total nesting effort and clutch parameters.

Given the number of sources of possible variation and the lack of information about them, complex analyses are inappropriate. The predicted age structure cannot usefully be translated into a size structure, because information on the marked individual variation in
growth patterns is not available for each of the females in the population. Therefore, a simple, perhaps somewhat crude, analysis was undertaken.

Available information suggests that all female *C. johnstoni* are mature at 15 years of age or approximately 80 cm SVL (Webb, Buckworth and Manolis 1983b, d; Smith and Webb 1985). The smallest known mature female was 66 cm SVL, though her age is unknown. Females begin maturing at least by the age of 9 years, though it is possible that some may mature earlier. For the purposes of this analysis, it is assumed that females may mature between the ages of 8 and 14 years and that they are fully mature from 15 to 50 years of age. An 80 cm SVL female is predicted to lay eggs of a mean weight of 67.9 g. Therefore, any clutches of eggs with a mean weight of less than 68.0 g are assumed to have come from maturing females (i.e. those between 8 and 14 years of age). Any clutches with a mean egg weight of greater than, or equal to, 68.0 g are assumed to have come from mature females (i.e. those between 15 and 50 years of age).

The above assumptions allow available clutches to be divided into two groups and from the predicted age structure (Smith and Webb 1985) it is possible to divide the female population into two comparable groups. On the basis of the estimates of the number of crocodiles in the pools under study (see Table 2.1) and the total population size, it was determined that approximately 24% of the total McKinlay River population was being examined. Thus the total age structure was scaled down to 24% of its predicted size.
The number of nests in a particular class was divided by the number of females in the appropriate class. Where the number of nests examined was less than the total nesting effort (eg. 1983, Table 4.8), the number of nests in each class was scaled up by the ratio of the total nesting effort divided by the total number of nests measured. This scaled number was divided by the number of females in that class, multiplied by 100 and termed the corrected percentage nesting (corrected percentage, Table 4.8).

The corrected percentage nesting varied between 22.86 and 54.44% for the maturing class and between 18.75 and 62.22% among the mature class. When the data for the five years were pooled, 37.74% of females in the maturing class nested annually and 45.74% of the mature class nested annually. Of the total female population, 41.77% nested annually.

These results are contrary to those for *C. johnstoni* (Webb, Buckworth and Manolis 1983d; Smith and Webb 1985) where it has been calculated that 28.6% of females between 9 and 11 years of age and 84.4% of females between 15 and 45 years of age breed annually. Both these estimates are considered to have ranges of ± 10% and thus that for maturing females may be congruent whereas the estimate for mature females is not. However, the estimate of Smith and Webb (1985) for mature females includes only those less than 46 years of age.

The percentages for each class were examined against temperatures at Middle Point for the months April-July and also for the total rainfall in the November-May period (Table 4.9). None of the
correlations proved to be significant, a point that will be returned to in the discussion.

4.2.6 THE CORRELATION STRUCTURE OF NESTING

We have already seen that larger females lay larger clutches of larger eggs and that they tend to lay them earlier in the nesting season than do smaller females. Other important and significant correlations exist. Among a sample of 48 nests for which day of laying and day of hatching was precisely known, day of laying was correlated with total incubation time ($r = -0.5393; df = 46; 0.001 > P$) and hence with day of hatching ($r = 0.5759; df = 46; 0.001 > P$). Clutches laid early tend to incubate for longer, and hence must hatch relatively late. The relatively long incubation period may be expected to be related to lower incubation temperatures. In some substrates, egg weight is positively correlated with egg depth (e.g. medium sands; $r=0.5086; df= 84 ; 0.001 > P$).

In 1985, an attempt was made to break this correlation structure. It is impossible to change the relationship between egg size and day of laying. However, by altering egg depth, and hence temperature, it is possible to incubate larger eggs more rapidly than usual, and have them hatch earlier. To accomplish this, all clutches from Sites other than Three were relocated to Site Three. They were buried in a small area of homogeneous substrate, thus removing all variables other than day of laying and depth. Unfortunately, the majority of these nests suffered predation by goannas (*Varanus gouldii*), and thus the experiment produced no useful results in this specific connection.
4.3 DISCUSSION

4.3.1 THE RELATIONSHIP BETWEEN FEMALE SIZE AND CLUTCH PARAMETERS

Relationships between clutch parameters and female size either have been shown to exist or else been suggested to exist in *Caiman crocodilus* (Staton and Dixon 1977), *Crocodylus novaeguineae* (Graham 1981; Hall 1983; Cox 1984), *C. niloticus* (Cott 1961; Graham 1968; Hutton 1984), *C. johnstoni* (Webb, Buckworth and Manolis 1983d), and *Alligator mississippiensis* (Wilkinson 1983; Ferguson 1985). Such relationships are usually highly variable and rarely quantified. The relationships derived here, though obtained from females of three geographically distinct populations is a remarkably good fit, though this could well be a reflection of the limited nature of the data on which it was based (Fig. 4.1).

That clutch size and clutch mass decline among particularly old females has been shown in *C. niloticus* (Graham 1968) and *A. mississippiensis* (Joanen and McNease 1980; Ferguson 1985), and is believed to occur in *C. johnstoni* (Webb, Buckworth and Manolis 1983d). On the basis of the SVL's predicted from the three clutch parameters (Figs. 4.25, 4.26) this does appear to be the case. However, the reduction in clutch size and mass is most likely to be related to age rather than size (Ferguson 1985; Lance 1987). Thus, the decline found here is most likely a reflection of the age rather than the size of the females concerned.
4.3.2 NEST SITES AND THEIR SELECTION

The nesting strategy of *C. johnstoni* appears to be unique among crocodilians. It is the only species not known to attend the nest during incubation (Webb, Buckworth and Manolis 1983d). As such, nest site selection in *C. johnstoni* may be less constrained than in other species where the female spends long periods of time at the site.

*Crocodylus niloticus*, another hole nesting species, apparently selects nest sites in relation to shade, suitable soil, proximity to water and degree of slope of the shore (Mohda 1967) and perhaps also soil moisture content (Pooley 1969). Of these factors, shade, proximity to water and degree of slope of the shore would appear to relate more to the comfort of the female than to the ecology of the eggs. Indeed, in the limited study of nest site selection in *C. johnstoni* presented here, neither shade nor proximity to water were found to be significant correlates of nesting. This is not surprising since the nests sites examined were generally close to the water, and because females of *C. johnstoni* do not appear to return to the nest until hatching is imminent. Where the nest sites are some distance from the pool (e.g. > 40 m at Site 5), the crocodiles must often negotiate quite steep inclines between the pool and nest site, though the degree of slope of the shore adjacent to nest sites is highly variable.

The avoidance of grassed areas by female *C. johnstoni* when selecting a nest site is most likely to be a reflection of the ease of
digging at a particular site: a substrate is easier to dig in if it is not consolidated by vegetation. The model for nest site selection at Site 3 suggests that suitable non-grassed sites are not limiting (there are more present than are utilised), thus absolute avoidance of grassed areas is possible. Should the entire bank become grassed, then it is possible that females may be forced to nest elsewhere.

At the upstream site shown in Figs. 4.14 and 4.15, which became completely grassed, females ceased nesting on that bank. Whether the lack of suitable substrate would cause a cessation of nesting is unknown. However, it could influence the selection of the pool in which the females spend the dry season.

The influence of temperature on nest site selection may be very important. Though it has been suggested as a probable influence (Webb and Smith 1984; Ferguson 1985), this is the first documentation of such an influence in crocodilians. Temperature has been shown to be a cue for nest site selection in the loggerhead turtle (Stoneburner and Richardson 1981) and the painted turtle, *Chrysemys picta* (Schwarzkopf and Brooks 1987). Temperature appears to act as a cue in the same manner in both *C. johnstoni* and the loggerhead: sites below some threshold temperature are unacceptable whereas those above that threshold are acceptable.

The function of nest site selection in *C. johnstoni* is unknown. In *Chrysemys picta*, nest site selection apparently functions to maximise embryo survivorship (Schwarzkopf and Brooks 1987). The same appears to be true in the lizards *Iguana iguana* (Rand 1968) and
Conolophus subcristatus (Werner 1983). Given that the sex ratio of *C. johnstoni* hatchlings depends primarily on the day the eggs are laid (Section 5.2.5), it is unlikely that nest site selection has any relationship to sex ratio selection. Thus, nest site selection probably functions to maximise embryo survivorship.

The two stage model of nest site selection goes part way to explaining the pre-nesting digging behaviour of *C. johnstoni*. Digging is predicted to occur at a larger range of temperatures than is nesting. This suggests that, while females may detect temperature at the surface, it is not a particularly accurate guide to sub-surface temperatures. Pre-nesting digging occurs up to two weeks before nesting (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984). Given the apparent relationship between digging, nesting and temperature, it is possible that the delay between first digging and first nesting may reflect the time required for substrate temperatures at 20 cm below the surface to increase from 28°C to 30°C. Minimum temperatures at Middle Point increase an average of 5.6°C over the period July-September and maximum temperatures increase an average of 3.6°C during the same period. Nest temperatures and their variation will be considered further in Chapter 5.

Considerable interest exists in the influence of substrate water potential on the ecology of reptile embryos. While in the laboratory it is possible to vary temperature and water potential independently, under field conditions, they can be expected to co-vary. Thus, substrate temperature and water potential can be expected to be highly related in *C. johnstoni* nests, and selection on the basis
of temperature will automatically also be on the basis of water potential. For a general discussion of the relationship between soil temperature and water see Rose (1968), Wierenga and de Wit (1970), Hillel (1971, 1977, 1980a, b, 1982), Kirkham and Powers (1972), Westcot and Wierenga (1974). Packard et al. (1985) provide a useful discussion of the daily and seasonal variation of hydric conditions and temperature in the nests of the turtle Chelydra serpentina.

That none of the available variables was significantly related to nest site selection at Site 5 may simply reflect the small number of data points there. However, it is possible at Sites which exhibit so little variability, that nest site selection is effectively random. What identifies that area in which nesting occurs from those adjacent is unknown, although proximity to the pool in which the females spend their time is the most obvious.

4.3.3 THE TIME OF NESTING

The reproductive cycle of crocodilians is tightly coupled to their environment (Lance 1987). The time of nesting of A. mississippiensis is known to be related to ambient temperatures in the preceding three months (Joanen 1969; Joanen and M^CNease 1979, 1981b; Joanen et al. 1981; Wilkinson 1983), and water levels and rainfall relate to time of nesting in C. niloticus (Cott 1957; Mohda 1967; Pooley 1969; Blomberg 1977), C. porosus (Webb, Sack, Buckworth and Manolis 1983), and Caiman crocodilus (Staton and Dixon 1977). It is therefore not surprising that some aspects of the environment should relate to time of nesting in C. johnstoni.
That time of nesting should be most highly correlated with temperatures experienced three months before nesting is reasonable. Follicular growth and vitellogenesis are initiated some three months prior to nesting in *A. mississippiensis* (Lance 1987). Given the vast similarities among crocodilians in their reproductive biology (Ferguson 1985), *C. johnstoni* can be expected to follow the same pattern.

### 4.3.4 VARIATION IN CLUTCH PARAMETERS WITH RESPECT TO DAY OF LAYING

As previously reported, within a nesting season, there is a general though variable decline in clutch size, clutch mass and mean egg weight in *C. johnstoni* (Webb, Buckworth and Manolis 1983d). These trends are supported here, and it is concluded that larger females tend to lay earlier in the nesting season than do small females. This trend has also been reported in *Caiman crocodilus* (Staton and Dixon 1977), *A. mississippiensis* (Ferguson 1985) and *C. niloticus* (Hutton 1984).

SVL_{ewt} is more highly correlated with the proportion of the nesting season completed than with day of year. Thus, it would appear that whenever the nesting season occurs, larger females still nest earlier. The relationship between SVL_{ewt} and P Day predicts that the first females to nest are approximately the average maximum size in the population and that the last are about the size of first maturity. This appears to describe the mean age-size relationship derived for this population (Webb, Buckworth and Manolis 1983b). If this is correct, then time of nesting may be more closely related to age than
size. Thus, the variability in the relationship between size and day of laying is a reflection of the variability in the age-size relationship.

The reasons for large females nesting before small females are unknown. It has been suggested that a social hierarchy exists such that large females mate early with large males whereas small females mate later with large or small males (Ferguson 1985). Behavioural data are lacking for C. johnstoni, but such hierarchies certainly exist in other species (Lang 1987) and therefore may well exist in C. johnstoni. Alternatively, larger females may be more efficient thermoregulators than small females (Smith 1975). Thus a large female may more easily attain a body temperature appropriate to follicular development than can a small female. The effect will be compounded by a social hierarchy since large, more dominant females will have better access to basking sites than will small females. Thus the relationship between female size and day of laying may primarily reflect the fact that large females can complete follicular growth and vittelogenesis more rapidly than can small females.

There is no obvious reason why it should be an age based rather than size based relationship. However, the onset of both reproductive maturity and senescence are probably age, rather than size, related in wild females (Webb, Buckworth and Manolis 1983d; Ferguson 1985; Lance 1987).
4.3.5 VARIATION IN CLUTCH PARAMETERS AND TOTAL NESTING EFFORT AMONG YEARS

Clutch parameters vary considerably among years (Figs. 4.29, 4.30 and 4.31). Given the relationships between female size and clutch parameters, this variation partly reflects changes in the size structure of the breeding females. This contention assumes that the relationships between female size and clutch parameters do not vary markedly between years. Such variation has been suggested to occur in *A. mississippiensis* but is unconfirmed (Deitz and Hines 1980; Ferguson 1985).

The simple analysis, which expressed nests laid as a percentage of the number of females in a class, failed to demonstrate any relationship with temperature or rainfall. Variation in nesting effort in response to weather patterns has been reported for other crocodilian species (*C. porosus*; Webb, Sack, Buckworth and Manolis 1983: *A. mississippiensis*; Joanen and McNease 1981b; Wilkinson 1983), but its existence cannot be confirmed here. That such an effect occurs in *C. johnstoni* is highly likely. The failure to detect it here is most probably a reflection of the crudeness of the analysis employed.
Table 4.1. The relationship between female size and clutch parameters for eight *C. johnstoni*.

<table>
<thead>
<tr>
<th>Snout-Vent Length (cm)</th>
<th>Mean egg weight (g)</th>
<th>Clutch size (N)</th>
<th>Clutch mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>88.5</td>
<td>74.3</td>
<td>14</td>
<td>940.8</td>
</tr>
<tr>
<td>90.2</td>
<td>69.6</td>
<td>13</td>
<td>893.2</td>
</tr>
<tr>
<td>63.0</td>
<td>56.3</td>
<td>6</td>
<td>338.1</td>
</tr>
<tr>
<td>61.0</td>
<td>58.2</td>
<td>4</td>
<td>262.8</td>
</tr>
<tr>
<td>77.6</td>
<td>66.2</td>
<td>8</td>
<td>529.6</td>
</tr>
<tr>
<td>68.5</td>
<td>66.7</td>
<td>9</td>
<td>600.3</td>
</tr>
<tr>
<td>103.0</td>
<td>-</td>
<td>-</td>
<td>991.2</td>
</tr>
<tr>
<td>96.6</td>
<td>-</td>
<td>14</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 4.2. The predicted probability (± SE) of *C. johnstoni* nesting within 2 m of data points classified by the presence of grass and by temperature.

<table>
<thead>
<tr>
<th></th>
<th>&lt; 30°C</th>
<th>≥ 30°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass</td>
<td>0.0091 ± 0.0121</td>
<td>0.0695 ± 0.0666</td>
</tr>
<tr>
<td>No Grass</td>
<td>0.1315 ± 0.0865</td>
<td>0.5514 ± 0.1108</td>
</tr>
</tbody>
</table>
Table 4.3. Mean and median day of nesting for 146 *C. johnstoni* nests over a five year period. Day of nesting is relative to 31 July. Thus, Day 1 is August 1.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean ± SD</th>
<th>Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>32</td>
<td>19.56 ± 5.09</td>
<td>20</td>
</tr>
<tr>
<td>1982</td>
<td>27</td>
<td>21.52 ± 5.47</td>
<td>19</td>
</tr>
<tr>
<td>1983</td>
<td>29</td>
<td>31.79 ± 5.25</td>
<td>31</td>
</tr>
<tr>
<td>1984</td>
<td>31</td>
<td>20.19 ± 5.49</td>
<td>21</td>
</tr>
<tr>
<td>1985</td>
<td>27</td>
<td>27.33 ± 4.24</td>
<td>26</td>
</tr>
</tbody>
</table>
Table 4.4. Predicted mean ages and sizes of breeding female *C. johnstoni* for the period 1980, 1982–85.

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean age (years)</th>
<th>Mean size ± SD (cm SVL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>22.36</td>
<td>77.17 ± 18.24</td>
</tr>
<tr>
<td>1982</td>
<td>21.22</td>
<td>83.85 ± 17.40</td>
</tr>
<tr>
<td>1983</td>
<td>21.35</td>
<td>86.76 ± 13.71</td>
</tr>
<tr>
<td>1984</td>
<td>21.16</td>
<td>85.05 ± 20.61</td>
</tr>
<tr>
<td>1985</td>
<td>21.10</td>
<td>76.80 ± 15.34</td>
</tr>
</tbody>
</table>
Table 4.5. Descriptive statistics of the distribution of *C. johnstoni* clutch size (eggs) for the years 1979, 1980 1982-85.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean ± SD</th>
<th>Skewness ± SE</th>
<th>Kurtosis ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979</td>
<td>15</td>
<td>12.33 ± 2.97</td>
<td>-1.0657 ± 0.5801</td>
<td>0.5788 ± 1.1209</td>
</tr>
<tr>
<td>1980</td>
<td>29</td>
<td>13.38 ± 2.87</td>
<td>-0.2046 ± 0.4335</td>
<td>-0.6761 ± 0.8452</td>
</tr>
<tr>
<td>1982</td>
<td>36</td>
<td>12.67 ± 3.11</td>
<td>0.2929 ± 0.3925</td>
<td>-0.7941 ± 0.7681</td>
</tr>
<tr>
<td>1983</td>
<td>15</td>
<td>12.60 ± 4.32</td>
<td>0.2113 ± 0.5801</td>
<td>-1.2566 ± 1.1209</td>
</tr>
<tr>
<td>1984</td>
<td>29</td>
<td>12.28 ± 3.75</td>
<td>-0.7942 ± 0.4335</td>
<td>1.4590 ± 0.8452</td>
</tr>
<tr>
<td>1985</td>
<td>23</td>
<td>10.48 ± 2.87</td>
<td>-0.2472 ± 0.4813</td>
<td>0.8593 ± 0.9348</td>
</tr>
<tr>
<td>TOTAL</td>
<td>147</td>
<td>12.35 ± 3.36</td>
<td>-0.2266 ± 0.2000</td>
<td>0.2320 ± 0.3974</td>
</tr>
</tbody>
</table>
Table 4.6 Descriptive statistics of the distribution of *C. johnstoni* clutch mass (g) for the years 1979, 1980 1982-85.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean ± SD</th>
<th>Skewness ± SE</th>
<th>Kurtosis ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979</td>
<td>15</td>
<td>816.52 ± 243.32</td>
<td>-0.5029 ± 0.5801</td>
<td>0.0382 ± 1.1209</td>
</tr>
<tr>
<td>1980</td>
<td>29</td>
<td>896.24 ± 271.77</td>
<td>0.3572 ± 0.4335</td>
<td>-0.2265 ± 0.8452</td>
</tr>
<tr>
<td>1982</td>
<td>36</td>
<td>890.40 ± 286.22</td>
<td>0.2824 ± 0.3925</td>
<td>-0.8126 ± 0.7681</td>
</tr>
<tr>
<td>1983</td>
<td>15</td>
<td>899.18 ± 370.12</td>
<td>0.3662 ± 0.5801</td>
<td>-0.9825 ± 1.1209</td>
</tr>
<tr>
<td>1984</td>
<td>29</td>
<td>858.85 ± 327.18</td>
<td>-0.2279 ± 0.4335</td>
<td>-0.1420 ± 0.8452</td>
</tr>
<tr>
<td>1985</td>
<td>23</td>
<td>690.88 ± 233.37</td>
<td>0.1523 ± 0.4813</td>
<td>-0.3199 ± 0.9348</td>
</tr>
<tr>
<td>TOTAL</td>
<td>147</td>
<td>847.47 ± 293.01</td>
<td>0.2170 ± 0.2000</td>
<td>-0.2378 ± 0.3974</td>
</tr>
</tbody>
</table>
Table 4.7 Descriptive statistics of the distribution of *C. johnstoni* mean egg weight (g) for the years 1979, 1980-1985.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
<th>Skewness</th>
<th>SE</th>
<th>Kurtosis</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979</td>
<td>15</td>
<td>65.31±6.75</td>
<td>-0.1296±0.5801</td>
<td>-0.7357±1.1209</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>29</td>
<td>66.00±8.20</td>
<td>0.0086±0.4335</td>
<td>-0.1100±0.8452</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1982</td>
<td>36</td>
<td>69.22±8.41</td>
<td>-0.6679±0.3925</td>
<td>-0.4336±0.7681</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>15</td>
<td>69.87±6.65</td>
<td>0.0143±0.5801</td>
<td>-0.8464±1.1209</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1984</td>
<td>29</td>
<td>68.84±9.41</td>
<td>-0.0343±0.4335</td>
<td>-0.0876±0.8452</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1985</td>
<td>23</td>
<td>65.56±6.60</td>
<td>-0.2798±0.4813</td>
<td>0.2989±0.9348</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>147</td>
<td>67.60±8.07</td>
<td>-0.1422±0.2000</td>
<td>-0.1759±0.3974</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.8. The numbers and proportions of maturing, mature and total female *C. johnstoni* breeding in the years 1980, 1982-85.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of females</td>
<td>Number of nests</td>
<td>Corrected percentage</td>
<td>Number of females</td>
<td>Number of nests</td>
</tr>
<tr>
<td>Maturing</td>
<td>49</td>
<td>23</td>
<td>46.94</td>
<td>52</td>
<td>18</td>
</tr>
<tr>
<td>Mature</td>
<td>45</td>
<td>17</td>
<td>37.78</td>
<td>45</td>
<td>28</td>
</tr>
<tr>
<td>Total nests</td>
<td>94</td>
<td>40</td>
<td>42.55</td>
<td>97</td>
<td>46</td>
</tr>
<tr>
<td>Measured total</td>
<td>40</td>
<td></td>
<td></td>
<td>46</td>
<td></td>
</tr>
</tbody>
</table>
Table 4.9. Correlations between the proportion of maturing, mature and total female *C. johnstoni* breeding and mean monthly temperatures and yearly rainfall for the period 1980, 1982-85. The correlations have 3 degrees of freedom.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Maturing</th>
<th>Mature</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum April</td>
<td>-0.5613</td>
<td>0.1718</td>
<td>-0.3699</td>
</tr>
<tr>
<td>Maximum April</td>
<td>-0.1177</td>
<td>0.4010</td>
<td>0.5664</td>
</tr>
<tr>
<td>Minimum May</td>
<td>0.1308</td>
<td>-0.2006</td>
<td>-0.1446</td>
</tr>
<tr>
<td>Maximum May</td>
<td>0.5097</td>
<td>-0.0987</td>
<td>0.5566</td>
</tr>
<tr>
<td>Minimum June</td>
<td>-0.5279</td>
<td>0.5821</td>
<td>0.5014</td>
</tr>
<tr>
<td>Maximum June</td>
<td>-0.4068</td>
<td>0.5187</td>
<td>0.5430</td>
</tr>
<tr>
<td>Minimum July</td>
<td>-0.1142</td>
<td>0.0848</td>
<td>0.1213</td>
</tr>
<tr>
<td>Maximum July</td>
<td>-0.1083</td>
<td>0.2123</td>
<td>0.3595</td>
</tr>
<tr>
<td>Rainfall</td>
<td>0.3130</td>
<td>-0.1414</td>
<td>0.4970</td>
</tr>
</tbody>
</table>
Fig. 4.1. The relationships between *C. johnstoni* female size and mean egg weight (top), clutch size (middle) and clutch mass (bottom).
Fig. 4.2. A nesting bank at Site 1 where one female layed a nest in 1985. In this photograph, as in all others, nesting occurred approximately at the position defined by the investigator.

Fig. 4.3. A small low-lying sand bank at Site 1 which was usually used as a nest site by one female each year.
Fig. 4.4. A small low-lying sand bank at Site 4 which was usually used as a nest site by one female each year.

Fig. 4.5. A small low-lying sand bank at Site 4 which was used as a nest site by one female in 1985.
Fig. 4.6. The only known nesting area at Site 7.

Fig. 4.7. Colonial nesting site in the McKinlay River mainstream adjacent to Site 5.
Fig. 4.8. Colonial nesting site in the McKinlay River mainstream adjacent to Site 5.

Fig. 4.9. A bank of fine sand in the McKinlay River mainstream deposited in the 1984/85 wet season which was used as a nest site by one female. The majority of the bank including that section which contained the nest was washed away by early wet season rains.
Fig. 4.10. The colonial nesting bank at Site 3, 1978.
Photo G. Webb.

Fig. 4.11. The colonial nesting bank at Site 3, 1979.
Photo G. Webb.
Fig. 4.12. The colonial nesting bank at Site 3, 1983.

Fig. 4.13. The colonial nesting bank at Site 3, 1985.
Fig. 4.14. A small nesting bank in the upstream area of the McKinlay River in 1979. Photo G. Webb.

Fig. 4.15. The nesting bank shown in Fig. 4.14 but the photo was taken in 1985. Photo G. Webb.
Fig. 4.16. The distribution of day of laying of 146 C. johnstoni nests for the period 1980, 1982-85.
Fig. 4.17. The relationship between median day of laying and mean maximum temperature as recorded at Middle point. The line is the regression line of best fit (see text).
Median day of laying

Mean May maximum temp. (°C)
Fig. 4.18. The distribution of total clutch mass with respect to day of laying for the period 1980, 1982-85.
Day of laying (relative to 31 July)
Fig. 4.19. The relationship between the total mass of clutch C. johnstonei clutches and the day on which they were laid. The clutch of one egg (arrowed) was excluded from analyses. Open circles represent a coincidence of data points.
Fig. 4.20. The distribution of clutch size with respect to day of laying for the period 1980, 1982-85. Circled points represent a coincidence of data points.
Clutch size (number of eggs)

Day of laying (relative to 31 July)
Fig. 4.21. The relationship between the size of *C. johnstoni* clutches and the day on which they were laid. The clutch of one egg (arrowed) was excluded from analyses. Open circles represent a coincidence of data points.
Clutch size (No. of eggs)

Day of laying (relative to 31 July)
Fig. 4.22. The distribution of mean egg weight with respect to day of laying for the period 1980, 1982-85. Circled points represent a coincidence of data points.
Fig. 4.23. The relationship between the mean egg weight within *C. johnstoni* clutches and the proportion of the nesting season completed when they were laid. Open circles represent a coincidence of data points.
Fig. 4.24. The relationship between the mean egg weight within *C. johnstoni* clutches and the day on which they were laid. Open circles represent a coincidence of data points.
Fig. 4.25. The relationship between the difference in the snout-vent lengths (SVL) of individual females as predicted from clutch size and from egg weight ($SVL_{sc} - SVL_{ewt}$) and the SVL predicted from egg weight ($SVL_{ewt}$). Open circles represent a coincidence of data points. The line is that of no difference in SVL as estimated by egg weight and clutch size.
Fig. 4.26. The relationship between the difference in the snout-vent lengths (SVL) of individual females as predicted from clutch mass and from egg weight ($SVL_{cm}$ - $SVL_{ewt}$) and the SVL predicted from egg weight ($SVL_{ewt}$). Open circles represent a coincidence of data points. The line is that of no difference in SVL as estimated by egg weight and clutch mass.
Fig. 4.27. The relationship between the mean of three estimates of individual female's snout-vent length (SVL) and the day on which they nested. Open circles represent a coincidence of data points. The line is the regression line of best fit (see text).
Fig. 4.28. The relationship between the mean of three estimates of individual female’s snout-vent length (SVL) and the proportion of the nesting season completed when she nested. Open circles represent a coincidence of data points. The line is the regression line of best fit (see text).
Fig. 4.29. The frequency distribution of clutch size in the years 1979, 1980, 1982-85
Fig. 4.30. The frequency distribution of clutch size for the pooled sample of nests from 6 years.
Clutch size (no of eggs)
Fig. 4.31. The frequency distribution of clutch mass in the years 1979, 1980, 1982-85.
Fig. 4.32. The frequency distribution of clutch mass for the pooled sample of nests from 6 years.
Fig. 4.33. The frequency distribution of mean egg weight in the years 1979, 1980, 1982-85.
Fig. 4.34. The frequency distribution of mean egg weight for the pooled sample of nests from 6 years.
The histogram represents the distribution of mean egg weights among clutches. The x-axis indicates mean egg weight in grams, ranging from 48.4 to 88.0 g, while the y-axis shows the number of clutches. The histogram is skewed, with a peak at around 62.0 g.
Fig. 4.35. The behaviour of mean clutch mass, clutch size and egg weight among the years 1979, 1980, 1982-85.
It has previously been suggested that day of laying has an important role in determining the probability of survival of embryos and may also be correlated with their size (Bock and Smith 1984). It has already been shown that there is a relationship between the size...
CHAPTER 5

THE ECOLOGY OF EGGS AND EMBRYOS

5.1 INTRODUCTION

Embryological development is the most critical stage in the life history of *Crocodylus johnstoni*. It is characterised by extremely variable, and often low, survivorship, and it determines the sex of individuals (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984, 1987; Smith and Webb 1985; Webb, Beal, Manolis and Dempsey 1987). Also, there is a growing body of evidence that the incubation environment of crocodilians is a fundamental determinant of post-hatching growth and survival (Webb, Beal, Manolis and Dempsey 1987; Joanen et al. 1987). Thus, the importance of the incubation environment cannot be overstated.

Three major causes of embryonic loss have been identified in *C. johnstoni*: the predation of nests; flooding; and overheating (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984). Additional to these, a failure of the yolk rotation mechanism of the eggs may also be a cause of embryonic death (Webb, Manolis, Whitehead and Dempsey 1987; Webb, Manolis, Dempsey and Whitehead 1987).

It has previously been suggested that day of laying has an important role in determining the probability of survival of embryos and may also be correlated with their sex (Webb and Smith 1984). It has already been shown that there is a relationship between the size
of the female and the time at which she nests, the size of her eggs, and total incubation time (Chapter 4). Therefore, this Chapter will explore the causes of embryonic survivorship, and the environmental correlates of sex. In the discussion of embryo survivorship, two classes of mortality are recognised: primary and secondary mortality. The first identifies those eggs which are infertile or suffer predation, and thus whose survivorship cannot be related to the incubation environment. The second class identifies those embryos which initiated development but for some reason failed to develop into a normal hatchling. A summary of the fate of 805 eggs from 69 non-predated clutches from the years 1983-1985 appears in Table 5.1

5.2 RESULTS

5.2.1 PRIMARY MORTALITY

5.2.1.1 INCIDENCE OF PREDATION BY VARANIDS

In this study, predation by goannas accounted for 8 of 35 nests located in 1983 (23%), 10 of 47 in 1984 (21%), and 15 of 35 (43%) in 1985. The overall rate of nest loss to goannas was 33 of 117 nests (28%). *Varanus gouldii* was the only species of varanid to be seen active on the nesting banks. *Varanus mertensi* was sighted in the area, though was rarely seen actually on any nesting banks, and was never seen to be excavating *C. johnstoni* nests.

The timing of nest loss was extremely bimodal. Of the 25 nests taken by goannas, for which precise dates of predation are
available, 10 were taken within 10 days after laying, and the remaining 15 were taken between 63 and 83 days after laying (Fig. 5.1). Early loss was extremely Site dependent, whereas late loss occurred primarily in 1985 when all surviving nests had been moved to a single Site. Early loss occurred most commonly at only four of the seven major Sites. Over the three years of the study, those four Sites lost 19 of the 37 nests laid, whereas none of 80 nests laid at the other three Sites were predated upon early in incubation. All Sites, other than Site Two, were colonial nesting sites. None of the five nests located in the upstream area in 1983 suffered predation, and only two of those were at the same site.

Late nest loss occurred primarily in 1985, accounting for 14 nests in that year. A single nest suffered late predation in 1984 at Site Five. Of the 14 lost in 1985, nine had been moved to Site Three from other locations and placed in a very high density situation. The remaining five nests lost had been laid at that location.

To determine if there was any pattern of goanna predation other than a geographic one, two further analyses were undertaken. Firstly, the mean egg weights were calculated for nests located in 1983 and 1984. The 1985 data were not included as the pattern of nest loss was atypical and may have been an artefact of nest relocation.

Seventy seven nests were available from 1983-84 and 63 of these escaped predation by goannas. The mean egg weight for surviving nests was 69.76 ± 7.88 (± SD) whereas the mean egg weight for those clutches which suffered predation was 72.15 ± 4.66. The variances of
mean egg weight were unequal ($F_{62,13} = 2.8603$, $0.025 > P > 0.01$), but the means were not ($t = 1.502$, $df = 32$, $0.20 > P > 0.10$).

A second analysis was conducted to compare the cumulative number of nests taken by goannas against the cumulative number of nests laid (Fig. 5.2). The relationships were subjected to logistic regression analysis with the cumulative number of nests laid being the sole explanatory variable. In both 1983 and 1984, that explanatory variable was highly significant ($\chi^2 = 94.7950$, $0.005 > P$, and $\chi^2 = 61.5255$, $0.005 > P$ respectively). The residual deviances were $\chi^2_{14} = 6.2668$ ($0.975 > P > 0.90$) and $\chi^2_{16} = 3.1876$ ($P > 0.995$) respectively, indicating that the models were well fitted. The intercepts of the curves were not different ($-4.386 \pm 0.789$ (± SE) and $-2.456 \pm 0.528$ respectively) and nor were the slopes ($0.2080 \pm 0.0320$ and $0.2385 \pm 0.0441$ respectively). The results indicate that the rate of loss of nests to goannas is effectively constant throughout the nesting season with respect to the number of nests laid. Thus, most nests will be taken by goannas during that period when most nests are being laid.

The pattern of loss of clutches late in incubation was not investigated as it appeared to be an artefact of relocation.

5.2.1.2 THE INFLUENCE OF EGG SHAPE ON SUBSEQUENT DEVELOPMENT

Webb, Manolis, Whitehead and Dempsey (1987) have demonstrated that within 24 hours of laying, the yolk rotates within the eggs of crocodilians. Furthermore, it is possible for the embryo to die if located at the bottom of the egg when the egg is laid, thus making it
impossible for the yolk to rotate. Additionally, it is possible that particularly long and thin eggs may have their yolk rotation inhibited (Webb, Manolis, Whitehead and Dempsey 1987). Therefore, the relationship between egg shape and the subsequent development of those eggs was examined. An egg shape parameter was calculated as the simple ratio of egg length to egg width.

A number of comparisons were undertaken. These involved the classification of all eggs into one of three classes: those which exhibited some development; those where the entire clutch failed to exhibit development; and, those which themselves exhibited no development but where some members of the same clutch did develop at least to some extent.

The first of the comparisons was that of those eggs which showed at least some development with those which failed to develop yet were part of clutches which did show some development. This comparison indicated that those eggs which failed to develop were more variable in shape ($F_{55,452} = 2.1616, 0.001 > P$), and were also significantly smaller in their shape parameter ($t = 4.8665, df = 507, 0.005 > P$). A similar comparison of non-developing eggs from clutches which showed no development with non-developing eggs from clutches which did show some development indicated a difference in the variability of their shape parameter ($F_{55,57} = 2.0804, 0.01 > P > 0.001$), but failed to demonstrate any difference in the mean of their shape parameter ($t = 1.3368, df = 112, 0.20 > P > 0.10$). Therefore, eggs which showed no development but came from clutches where some development took place were different from eggs where some development
took place, yet were not different from those eggs in clutches where the entire clutch failed to show development. As a result, the two classes of egg failing to show development were pooled.

When all eggs that failed to show development were compared with those which did show some development, those showing no development were found to be more variable in shape \((F_{105,460} = 1.6022, 0.01 > P > 0.001)\). Also, non-developing eggs were significantly smaller in their shape parameter \((t = 6.8880, df = 565, 0.001 > P)\).

A comparison of egg weights in the two categories also provided some useful information. As with the shape parameter, the weight of non-developing eggs was significantly more variable than was the weight of developing eggs \((F_{105,564} = 1.4849, 0.01 > P > 0.001)\), and the mean weight of non-developing eggs was significantly smaller than the weight of developing eggs \((t = 8.9875, df = 669, 0.001 > P)\).

5.2.1.3 THE INFLUENCE OF EGG ANGLE ON SUBSEQUENT DEVELOPMENT

Within the nests of *C. johnstoni*, eggs lie at any angle between horizontal and vertical. It was considered possible that the angle at which an egg lay might be related to the survival of the embryo, i.e. that eggs lying vertical within the nest may have a lower probability of survival than eggs lying horizontal within the nest, as has been reported in *A. mississippiensis* (Joanen and McNease 1981a; Ferguson 1985). To examine this possibility, the angles of eggs within nests were compared for three classes of egg. All eggs resulting from clutches where none of the eggs showed any development were excluded.
The first class of eggs was that which produced normal hatchlings. The second class was that where the embryo failed to develop fully, and where no external cause of death could be found (e.g. the egg having suffered laying dents). The third class was that containing embryos which died at or around the time of hatching, or which hatched successfully but were abnormal.

Among the three classes of eggs, there were no significant differences with respect to the angle at which they had lain throughout incubation (data not shown because of negative result).

5.2.1.4 INCIDENCE OF INFERTILITY OR NO APPARENT DEVELOPMENT AND ITS RELATIONSHIP TO CLUTCH SIZE

The overall incidence of eggs failing to exhibit development is quite variable. As already noted above, this failure also tends to be associated with a longer and thinner egg, which is also below average weight.

Thirty six of 290 eggs (12.4%) examined in 1983 failed to show development, as did 43 of 355 (12.1%) in 1984 and 27 of 178 (15.2%) in 1985. Of the total of 106 eggs failing to show development, 43 eggs resulted from six clutches where all eggs failed to show development. These clutches are probably best considered to be infertile. Mean clutch size of those six clutches was 9.67 ± 1.9 (SD) eggs, which is considerably smaller than the previously reported clutches size (13.2 ± 3.2 eggs) of the McKinlay River population of C. johnstoni (Webb, Buckworth and Manolis 1983d).
5.2.1.5 INFLUENCE OF EGG SIZE ON THE SUCCESS OF VIABLE EGGS

It has been suggested that the size of eggs in the freshwater turtle *Chrysemys picta* has an intrinsic influence of the probability of successful completion of incubation (Gutzke and Packard 1985). A simple test of this was conducted with the available *C. johnstoni* data by modelling the occurrence of normal hatchlings against their egg weight. The analysis was structured such that those eggs which had suffered embryonic failure, died at or shortly after hatching, or had hatched and were abnormal were coded as zero (i.e. a 'failure'), and those animals which had hatched and were normal were coded as one (i.e. a 'success').

Logistic regression was used with 'success' as the dependent variable and factor transformed egg weight as the sole explanatory variable, and 510 individuals were available for the analysis. Egg weight failed to account for a significant amount of the total deviance $\chi^2 = 11.281, 0.50 > P > 0.10$ and thus does not appear to influence embryonic survival in *C. johnstoni* (data not shown because of negative result).

5.2.1.6 THE RELATIONSHIP BETWEEN SEX AND NON-SURVIVAL, AND THE AFFECT OF RELOCATION

Webb and Smith (1984) in their analysis of sex ratio and survival in *C. johnstoni* found that non-surviving embryos tended to be female. From a sample of 595 individuals examined in this study where sex could be ascertained, there was a non-significant difference in
the sex ratios of survivors (0.37, N=564) and non-survivors i.e. those assigned codes 4, 6, and 8 in Table 5.1 (0.26, N=31, $\chi^2_1 = 1.6052$, 0.50 > P > 0.10). The inclusion of the nine individuals which drowned in the nest in 1984 failed to increase the significance of the difference in sex ratio as all nine individuals were male.

A similar analysis indicated that there was no significant difference in the rate of survival of eggs in 1985 with respect to whether or not they had been relocated (data not shown because of negative result).

5.2.1.7 FLOODING

Much has been made of the importance of flooding as a negative influence among C. johnstoni clutches (Webb, Buckworth and Manolis 1983d, Webb and Smith 1984). In this connection, however, it should be recognised that 'flooding' is a composite phenomenon. There are three types of nest 'flooding', each with different likelihoods of occurrence. The least common form is true flooding, which is here defined as the inundation of a nest by a rising water table, such as would accompany increasing water levels in the associated pool. Given that water levels in pools drop throughout the dry season, it is not uncommon for nests to be 2 m above water level late in the dry season. Thus, it is rare for water levels in pools to rise sufficiently to inundate nests. This form of flooding was not observed in this study.

The second form of flooding is also uncommon. This occurs when nests are low-lying in a depression which subsequently fills with
water. Thus, the nests are drowned from above. The type of flooding was observed once in this study.

The final form of flooding is most common and accounts for all but one nest flooded in this study. This form of flooding is simply the formation of temporary creeks which run across nesting banks, cutting into them and washing away the eggs. This is the form of flooding illustrated by Webb, Buckworth and Manolis (1983d).

The data examined here suggest that flooding is not such a common occurrence. In complete data from 69 clutches, drowning was found to be the cause of death of only 9 of 805 embryos (1.1%). One clutch was in danger of being washed away in 1983 and was relocated to an incubator. That clutch was found to contain no viable eggs. Likewise, the single clutch washed away in early wet-season rains in 1984 contained no viable eggs. In the period 1983-85, flooding is known to have accounted for only 3 of the 117 clutches (2.6%).

5.2.2 THE THERMAL ENVIRONMENT OF CROCODYLUS JOHNSTONI NESTS

The thermal environment of C. johnstoni nests is critical to the survival and sex determination of the embryos. The significance of nest temperatures to crocodilian embryos is apparent from the information in Chapters 1 and 2. Therefore, it was considered important to obtain as much information about nest temperatures as possible.
All nests had a temperature recorded from near their centre with a calibrated mercury thermometer when they were discovered and when and if they were mapped. These temperatures may be indicative of whether a nest is generally warm or cool but, as they do not account for the marked diurnal temperature fluctuations and longer-term general warming that _C. johnstoni_ nests experience (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984), they cannot be considered indicative of the mean nest temperature. Additional to the initial and final temperatures recorded, the majority of nests had a varying number of temperatures recorded during incubation using either implanted calibrated thermistors, thermocouples or calibrated temperature transducers. The time of day at which these temperatures were recorded was effectively normally distributed around twelve noon.

These recordings generated some thousands of temperatures, which were reduced to 801 readings for 104 nests (Fig. 5.3). Where temperatures were recorded over a 24 hours period, the mean was calculated and used in the analysis. The mean time at which temperature was recorded was also used. The data available for the modelling of nest temperature were: the observed or mean nest temperature; the time of day relating to that recording; the minimum and maximum temperature recorded on that day and on the previous day at Middle Point; the day (relative to 31 July) on which the observation was made; the nest from which the observation originated; and, the year.

The modelling of soil temperatures is extremely complex. A sine model approximation is, however, adequate for most purposes.
Soil temperature can then be described by the equation:

\[ T = \bar{T} + A_0 \frac{\sin(\omega t - z/d)}{e^{z/d}} \]  

Eq. 5.1

where \( \bar{T} \) is the mean temperature, \( z \) is depth, \( \omega \) is the period \((2\pi/24)\), \( t \) is time in hours, \( A_0 \) is the amplitude of the temperature wave at the surface and \( d \) is the damping depth which is a characteristic of the soil (Kirkham and Powers 1972; Hillel 1982). The term \( z/d \) may be considered a constant for simple modelling purposes.

This formulation is an idealised one which does not allow for any temporal variation beyond the scope of 24 hours. A more generalised model can be formulated which allows for an annual cyclical variation in temperature according to the formula:

\[ T = \bar{T}_y + A_y \frac{\sin(\omega_y t - z/d_y)}{e^{z/d_y}} + A_d \frac{\sin(\omega_d - z/d_y)}{e^{z/d_d}} \]  

Eq. 5.2

where the subscripts \( y \) and \( d \) refer to yearly and daily variation respectively. \( \omega_y \) is the annual period \((2\pi/365)\). While this equation appears rather complex, it can be tractable in terms of statistical modelling. There are, however, complications with both equations. The temperature data available from \( C. \ johnstoni \) nests are from three different years and from nests in substrates classified into seven different types. Thus, it is accepted that to construct a single model for all the data will be an oversimplification.
The full equation (Eq. 5.2) in particular was not amenable to modelling, probably because the available data covered only a small part of the year. The result of this was that the daily variation could be modelled whereas the yearly variation could not. Therefore, an alternative approach was sought.

The influence of day was modelled first, with both linear and natural log (ln) terms of day being significant ($F_{1,591} = 2516.23, 0.005 > P$ and $F_{1,591} = 16.97, 0.005 > P$ respectively). Daily perturbations were expressed as the minimum and maximum temperatures observed at Middle Point on the day of observation and on the previous day. Of the four terms, three were significant. These were the minimum and maximum Middle Point temperature recorded on that day (MinD, $F_{1,591} = 311.95, 0.005 > P$ and MaxD, $F_{1,591} = 165.20, 0.005 > P$ respectively) and the maximum temperature recorded on the previous day (MacD-1, $F_{1,591} = 59.85, 0.005 > P$). Year was included as a three level factor and was highly significant ($F_{2,591} = 176.90, 0.005 > P$). Year was also significant in the model in four interaction terms. These were interactions with ln day ($F_{2,591} = 103.56, 0.005 > P$), minimum temperature on that day at Middle Point ($F_{2,591} = 38.99, 0.005 > P$), maximum temperature on the previous day at Middle Point ($F_{2,591} = 24.89, 0.005 > P$) and day ($F_{2,591} = 12.63, 0.005 > P$). Individual variation between nests was modelled next by the inclusion of nest number as a factor ($F_{101,591} = 8.18, 0.005 > P$). Nest number had significant interactions with a number of other variables, but only the most significant one was included as otherwise the model would have become totally unwieldy. The most significant interaction was that between nest and ln day ($F_{85,591} = 3.90, 0.005 > P$).
Diurnal variation was accounted for next, but not strictly in the terms of Eq. 5.1. As the trends in mean temperature had already been accounted for, the remaining variation may be described by

\[ T = A_0 \frac{\sin(\omega t - z/d)}{\exp(z/d)} \]  

Eq. 5.3

where the notation is the same as Eq. 5.1. The assumption that the mean trend had been accounted for was tested by including a term for the mean in the model. That term proved not to be significantly different from zero. However, it was noted that the amplitude of daily variation varied over time. Thus the model was modified to

\[ T = \ln \text{Day} \times A_0 \frac{\sin(\omega t - z/d)}{\exp(z/d)} \]  

Eq. 5.4

In this equation, the inclusion of modelled diurnal variation was highly significant (\( F_{1,591} = 303.78, 0.005 > \alpha \)).

During the modelling process, seven observations were removed as outliers. The final model accounted for 86.4% of the total variance in nest temperature. The inclusion of the seven points reduced the fit to 83.9% of the variance. No attempt was made to identify or partition the effects of any metabolic heat which may have been generated within the nests. The full model derived for nest temperature was:
Temperature = 23.64 - 7.25 x ln Day + 0.13 x Day + 0.65 x
MinD + 0.11 x MaxD + 0.27 x MaxD-1 + Year +
lnDay.Year + MinD.Year + MaxD-1.Year + Day.Year
+ Nest + Nest.lnDay + 2.46 x lnDay x -0.21 sin
(0.2618 x Hour - 0.48) / exp(0.48)  
Eq. 5.5

The coefficients for the main and interaction effects of year
appear in Table 5.2, and those for nest appear in Table 5.3. These
coefficients are necessary for predicting temperature for a given nest
at any time during incubation, and the predicted temperatures for
three such nests appear in Fig. 5.4.

Webb and Smith (1984) in a simple analysis of C. johnstoni
nest temperatures, found that temperatures of nests at laying and
hatching were uncorrelated, but that the increase in temperature over
incubation was predictable from the temperature at laying. The
predictive model obtained from Eq. 5.5 was used to estimate nest
temperature at midnight on the night of laying (T_l) and at midnight on
the day of hatching (T_h) for each of the 49 nests. The temperatures
were significantly correlated (r = 0.5193, df = 47, 0.005 > P) and the
temperature at hatching could be predicted from the relationship:

T_h = 5.14 + 1.003 x T_l (F_1,47 = 17.35, 0.005 > P).  Eq. 5.6

The relationship between T_l and the change in nest
temperature throughout incubation reported by Webb and Smith (1984)
was not found among these data. Rather the change in nest temperature
and T_l are uncorrelated (r = 0.0019, df =47, P > 0.975).
5.2.3 THE RELATIONSHIP BETWEEN SEX AND NEST TEMPERATURE

Incubation of *C. johnstoni* embryos under constant temperature produces only females at temperatures between 26.0°C and 30.0°C. Depending on the incubation method (see Webb, Beal, Manolis and Dempsey 1987), males may be produced at 31.0, 31.5, 31.7, 32.0, 32.5 and 33.0°C, though none of these temperatures produce only males. Temperatures above 33.0°C produce only females.

It has been shown that when these sex ratio data are considered against total incubation time, the pattern is far less variable, with males produced at mean total incubation times between 72.0 and 76.4 days but with only females produced at longer or shorter mean total incubation times (Webb, Beal, Manolis and Dempsey 1987). Regardless of the greater concordance between total incubation time and sex, constant temperature incubation studies have thus far failed to produce all males under any regime. Given that such a result may be obtained from field nests, it would appear that constant temperature incubation cannot replicate sex determination in the field.

The distribution of sex ratio with respect to total incubation time for 49 clutches examined over the period 1983-85 appears in Fig. 5.5. Included on the Figure are the data of Webb, Beal, Manolis and Dempsey (1987) for constant temperature laboratory incubation. As can be seen, males are produced over a larger range of total incubation time in the field than they are in the laboratory (70-85 days and 72-76.3 days respectively). Also, wholly male clutches were produced in the field and 18 of the 49 clutches (37%)
had sex ratios of greater than or equal to 0.50. The highest sex ratio produced in the laboratory was 0.31, whereas 25 of the 49 field clutches (51%) had sex ratios in excess of this (Fig. 5.5). However, there is considerable variation in the relationship between sex ratio and total incubation time in field nests. For example, 78 days total incubation produced sex ratios of both zero (one clutch) and one (two clutches) with an additional five clutches falling somewhere in between. An interpretation of the cause of this variation is that although two clutches may have the same total incubation time, they must have experienced different temperature regimes during incubation, or at least during the period of sex determination.

The model of nest temperature derived from Eq. 5.5 was used to investigate the relationship between temperature and sex in field nests. The nature of the relationship between varying temperature and sex determination is unclear. In one study, Bull (1985) examined sex determination in field nests of *Graptemys geographica*, *G. ouachitensis* and *G. pseudogeographica* with respect to recorded nest temperatures. Sex determination was related to hours per day above a critical temperature, to mean temperature and to the variance of nest temperature. The best association between nest temperature and sex occurred between weeks 4 and 7 of incubation.

Sex determination in *C. johnstoni* can be influenced by temperature in the range 4 - 65% of total incubation time (Webb, Beal, Manolis and Dempsey 1987). Thus, approximately the first two thirds of incubation may be temperature sensitive. The constant temperatures which may allow the development of males are within the range 31 -
33°C, with females falling outside that range. On the basis of these two results, a strategy was adopted for investigating the influence of nest temperature on sex determination.

Equation 5.5 was used to predict the hourly temperature in each of the 49 nests for which data were available. The precise time of laying was unknown, and was assumed to be twelve midnight on the night of laying. The mean temperature and the percentage of time spent between 31 and 33°C was calculated for each 10% of the total incubation period of each clutch. The total incubation time of each clutch was divided into 10% sections for two reasons: 1, there was marked variation in total incubation time; and 2, the timing of sex determination appears to vary with temperature of incubation. While the use of 10% periods does not completely remove these effects, it certainly reduces the biases to a large extent.

The influence of mean temperature may be expected to be parabolic in that the probability of males being produced will increase from low temperatures to some maximum and then decrease with higher temperatures. Thus, the mean temperature was also calculated as its square. The influence of hours spent between 31 and 33°C may be expected to be linear.

Logistic regression was used to examine the influence of the three parameters on sex determination. Each 10% of total incubation time was treated separately, and the $\chi^2$ attributable to fitting each of the parameters in each of the ten subsections of incubation appears in Fig 5.6.
The influence of mean temperature is very marked in early incubation, but subsequently declines. It does, however, increase again in the later stages of incubation. This rise in significance is unlikely to be related to sex determination, as there is no evidence that sex determination can be influenced by temperature so late in incubation. It is most likely a reflection of the predictability (serial correlation) of temperature throughout incubation. The square of mean temperature displayed a similar pattern throughout incubation (Fig. 5.6), though it was most important between 20 and 30% of incubation and was unimportant between 60 and 70% of incubation. Of the variables considered, the square of mean temperature between 20 and 30% of incubation was the most significant.

Hours spent between 31 and 33°C was significantly related to sex between 20 and 60% of incubation. The hours spent in that range in the period of 30 to 50% of incubation was the most significant. The importance of both mean temperature and hours spent between 31 and 33°C was investigated further by constructing a model for determination. Since data on substrate type (as a seven level factor) and mean depth were available for the nests this was evaluated in the model.

Mean temperature in the 20-30% period of incubation was fitted to the model first, as it was the most significant of the available variables both in parabolic ($\chi^2_1 = 98.8697, 0.005 > P$) and linear ($\chi^2_1 = 29.7430, 0.005 > P$) terms. After the inclusion of mean temperature in the 20-30% period, no other terms of mean temperature were significant. given that additional terms of mean temperature were
not significant, it was clear that additional parameters were required: it is known that sex is determined over a longer period than 10% of incubation (Webb, Beal, Manolis and Dempsey 1987). The interpretation of the significance of the 20-30% period was that appropriate temperatures during that period allowed the initiation of a male producing development trajectory. Thus it was considered likely that the pattern of temperature change after that period was crucial to the final production of males. Therefore, the change in mean temperature was examined next, and for each 10% period was coded as a five level factor. Of the available periods, the change in mean temperature between 20-30% and 30-40% of incubation as well as the change in mean temperature between 30-40% and 40-50% of incubation were both highly significant ($\chi^2_4 = 36.8853$, $0.005 > P$ and $\chi^2_4 = 30.1051$, $0.005 > P$ respectively). Additional to these terms was a significant influence of substrate ($\chi^2_6 = 39.7524$, $0.005 > P$) and a significant interaction between the two expressions of change in mean temperature ($\chi^2_8 = 38.4705$, $0.005 > P$). The residual deviance was 15.4036 and, with an assumed $\chi^2_{20}$ distribution, is not significant (0.90 > $P$ > 0.50). The model may thus be considered a good fit.

Given the complexity of the final model, the behaviour of all variables will not be considered. In particular, the interaction between the two expressions of change in mean temperature are difficult to visualise. The behaviour of sex ratio in terms of mean temperature in the 20-30% period when all other variables assume their mean value is shown in Fig. 5.7. As can been seen, males tend to be produced at intermediate temperatures whereas females are produced at more extreme temperatures. Apart from the fact that the model
correctly predicts the production of wholly male clutches, these results confirm constant temperature laboratory studies.

Table 5.4 summarises the behaviour of sex ratio with respect to change in mean temperature between the 20-30% and 30-40% periods and the change in mean temperature between the 30-40% and 40-50% periods. When these summary data are plotted (Fig. 5.8), it becomes clear that there is a single basic pattern: moderate or little change in temperature in the first period followed by a moderate change in the second period will produce males. Thus, extreme changes (within the range of the data) in the first period require similar changes, though in the opposite direction, in the second period to produce males.

5.2.4 THE RELATIONSHIP BETWEEN NEST TEMPERATURE AND TOTAL INCUBATION TIME

Given that there is considerable variance in the relationship between total incubation time and sex ratio (Fig. 5.5), but closer agreement between sex ratio and particular temperatures during incubation, it is possible that the overall mean temperature is not closely related to total incubation time as is that temperature experienced during some particular period of incubation. However, when total incubation time is plotted against mean temperature during incubation (Fig. 5.9), there is a clear association and significant correlation ($r=-0.6173, 0.01 > P$). The available data for temperatures during incubation where used to determine if any particular period had a major influence on total incubation time. Of the 10 time periods
tested, the mean temperature experienced between 20-30% of incubation was the most significant. The observed relationship between mean temperature in the 20-30% period and total incubation time appears as Fig. 5.10. Moreover, with terms for that period included, no other term expressing nest temperature reached significance. The mean temperature experienced in the 20-30% period was significant as both linear \( F_{1,46} = 62.52, 0.005 > P \) and \( \ln \ (F_{1,46} = 4.26, 0.05 > P > 0.025) \) terms. The overall model accounted for 57.4% of the total variance in total incubation time.

As can be seen (Figs. 5.9, 5.10), three clutches appear to be outliers to the general pattern. Careful investigation did not indicate why this was so. That the three clutches clustered together suggested a systematic error of some sort, although none could be identified. The clutches were not excluded from the analysis.

5.2.5 THE RELATIONSHIP BETWEEN SEX AND DAY OF LAYING

It has previously been suggested that day of laying influences the sex of the resulting hatchlings. The model of nest temperature derived above was remodelled, removing the nest effect and the interaction between nest and ln\( \text{day} \). This model was then used to predict temperatures which in turn were used to predict the sex ratio of an hypothetical clutch of eggs. The clutch was assumed to have a total incubation time of 78 days, as the mean incubation time for a sample of 50 nests was 78.52 days. Day of laying was varied over the range known for each of the three years (1983: 25-40; 1984: 10-30; 1985: 18-36). The model used for predicting sex ratio was simplified
by the removal of the factor for substrate type and the interaction term. Substrate type was removed, because the substrate in which the hypothetic clutch was laid was unknown. The interaction term was removed because it made the prediction process more simple.

The predicted sex ratios appear in Fig. 5.11. As can be seen, there is a nett tendency for females to be produced from clutches laid early and late in the nesting season. Males are generally produced from those clutches laid in the middle of the nesting season.

5.2.6 THE RELATIONSHIP BETWEEN NEST TEMPERATURE AND THE INCIDENCE OF NORMAL HATCHLINGS

The clutches examined above were reanalysed, with the variable of interest being that number of eggs which produced normal hatchlings versus that number which did not. The statistical methods employed are those above. The explanatory variables evaluated in this case were somewhat different to those above. Extremes of constant temperature have been shown to be related to developmental abnormalities and low survivorship during incubation. Therefore, it is likely that it is the extremes of temperature rather than the mean that will be related to survivorship in the field. Consequently, four new variables were calculated from the model of nest temperatures: percent of time spent below 28°C and the percent of time spent above 32, 34 and 36°C respectively.

Of the 486 eggs represented by the 49 clutches, a total of 427 (87.86%) produced normal hatchlings. From a modelling viewpoint,
this is not particularly good, as the model must predict the occurrence of an effectively rare event. However, the final model derived provided a very good fit to the data, though it may have limited utility for prediction because it deals with a rare event.

Both substrate type and mean egg depth were found to be significant ($\chi^2_6 = 33.3782, 0.005 > P$ and $\chi^2_1 = 6.2392, 0.025 > P > 0.01$ respectively). Also significant was an interaction between substrate type and depth ($\chi^2_5 = 17.8594, 0.005 > P$). Of the measures of mean temperature and time spent above and below various temperatures, only the percentage of time spent below 28°C between 80 and 90% of incubation proved significant. The coefficient for depth was positive, indicating improved survivorship with depth. The predicted relationship between depth and survivorship appears in Fig. 5.12. As can be seen, the influence is minor. The coefficient for the temperature term was also positive, indicating increased survivorship with increasing time spent at low temperatures late in incubation. The predicted relationship between temperature and survivorship appears in Fig. 5.13. As with the effect of depth, the influence of temperature is minor.

Substrate type was the most important of the influences on embryonic survival. As can be seen (Table 5.5), medium/coarse sands and sand/humus substrates were associated with lowered survivorship of embryos. The model had a residual deviance of 29.2330 with a $\chi^2_{31}$ distribution ($0.90 > P > 0.50$) which indicates that the model was a good fit.
5.2.7 THE DETERMINANTS OF HATCHLING SIZE

The size of a hatchling may be related to its probability of survival (Chapter 6). For this reason, it is of particular interest to examine the determinants of hatchling size. Three measures of size were utilised: residual yolk weight, yolk-free hatchling weight (total hatchling weight minus yolk weight) and head length. The aim of the analysis was not to derive simple predictive equations for hatchling size, but rather to explore as fully as possible those aspects of the incubation environment which exerted an influence on size.

Residual yolk weight was highly related to egg weight ($F_{1,310} = 429.50, 0.005 > P$). Temperature in the first 10% of incubation ($T_{10}$) was highly related to residual yolk weight ($F_{1,310} = 22.98, 0.005 > P$), as was the change in mean temperature over the entire course of incubation ($\Delta T$, $F_{1,310} = 45.10, 0.005 > P$). Substrate type was also significantly related to residual yolk weight ($F_{6,310} = 24.05, 0.005 > P$). Total incubation time and egg depth also proved significant ($F_{1,310} = 50.22, 0.005 > P$ and $F_{1,310} = 25.66, 0.005 > P$ respectively) as did the interaction terms between substrate type and total incubation time ($F_{5,310} = 20.03 > P$), substrate type and egg weight ($F_{6,310} = 8.56, 0.005 > P$) and between substrate type and egg depth ($F_{6,310} = 4.37, 0.005 > P$). The full model accounted for 72.0% of the total variance in residual yolk weight. The fitted relationship was:

\[
\text{Residual yolk weight} = 18.71 - 0.0042 \times \text{Egg weight} - 0.4085 \times T_{10} + 0.1230 \times \Delta T + \text{Substrate} - 0.0301 \times \text{Incubation time} + \text{Substrate.Egg weight} + \text{Substrate.Depth Eq. 5.7}
\]
The coefficients for Substrate, Substrate.Incubation time, Substrate.Egg weight and Substrate.Depth all appear in Table 5.6.

Hatchling yolk-free weight was related to similar environmental variables. Egg weight, ln ΔT and ΔT were all highly significant (F_{1,301} = 428.47, 0.005 > P, F_{1,301} = 104.53, 0.005 > P, and F_{1,301} = 22.27, 0.005 > P respectively). Substrate type, incubation time and depth were also all significantly related to hatchling yolk-free weight (F_{6,301} = 8.38, 0.005 > P, F_{1,301} = 26.21, and F_{1,301} = 9.92, 0.005 > P respectively). Significant interactions existed between incubation time and substrate type (F_{5,301} = 22.03, 0.005 > P), between ΔT and substrate type (F_{5,301} = 16.25, 0.005 > P), between ln ΔT and substrate type (F_{4,301} = 10.86, 0.005 > P), between depth and substrate type (F_{6,301} = 4.28, 0.005 > P), and between egg weight and substrate type (F_{6,301} = 2.54, 0.025 > P 0.01). The full model accounted for 72.3% of the total variance in hatchling yolk free weight. The fitted model was:

Hatchling yolk-free weight = 76.40 + 0.2595 x Egg weight - 16.90 x ln ΔT + 5.13 x ΔT + Substrate - 0.7027 x Incubation time + 0.1546 x Depth + Substrate.Incubation time + Substrate.ΔT + Substrate.In ΔT + Substrate.Depth + Substrate.Egg weight

Eq. 5.8

The coefficients for the main effect of Substrate, and the interaction terms Substrate.Incubation time, Substrate.ΔT, Substrate.In ΔT, Substrate.Depth and Substrate.Egg weight are given in Table 5.7.
Head length proved less tractable in terms of modelling than did either residual yolk weight or hatchling yolk-free weight. Egg weight was the most significant correlate of head length \( (F_{1,314} = 85.96, 0.005 > P) \). Ln ΔT and ΔT were both highly significant \( (F_{1,314} = 23.65, 0.005 > P \) and \( F_{1,314} = 20.53, 0.005 > P \) respectively). Substrate, ln Incubation time and Incubation time were also highly significant \( (F_{6,301} = 10.33, 0.005 > P, F_{1,301} = 10.77, 0.005 > P \) and \( F_{1,301} = 5.31, 0.005 > P \) respectively). Significant interaction terms existed between Substrate and ln Incubation time \( (F_{5,301} = 1408, 0.005 > P) \), Substrate and Δt \( (F_{5,301} = 4.16, 0.005 > P) \) and between Substrate and ln ΔT \( (F_{4,301} = 8.88, 0.005 > P) \). The full model accounted for 47.8% of the total variance in head length and was:

\[
\text{Head length} = 17.2 + 0.0053 \times \text{Egg weight} - 0.138 \times \ln \Delta T + 0.0381 \times \Delta T + \text{Substrate} - 3.68 \times \ln \text{Incubation time} + 0.0294 \times \text{Incubation time} + \text{Substrate.ΔT} + \text{Substrate.} \ln \Delta T
\]

Eq. 5.9

The coefficients for Substrate, Substrate. ln Incubation time, Substrate. ΔT and Substrate. ln ΔT appear in Table 5.8.

5.2.8 HATCHING

The design and intent of this study necessarily means that little detailed information on hatching was collected. Some casual observations of interest were, however, obtained.
Firstly, the hatching of a nest by an adult was not often accomplished in a single night. On numerous occasions it was observed that an adult would partially excavate a nest, but not to the level of the eggs. Any such nest not opened by me the following day would be completely excavated by a crocodile the following night. It was also observed on a smaller number of occasions that the crocodile would partly excavate the nest and remove a number of hatchlings and then re-cover the remainder of the clutch - presumably to return the following night to complete the excavation. On one occasion only, a crocodile is known to have attempted excavation of a nest during daylight hours. This occurred in 1985 when a nest was visited at 2 pm and found to be calling. When revisited for mapping at 5 pm, the nest was found to have been partly excavated, though not down to the level of the eggs.

Perhaps the most important observation concerning hatching relates to clutches relocated to Site Three. On five occasions, such clutches were found to have been partly excavated by adult crocodiles: crocodiles which could not have been parents of the clutches.
5.3 DISCUSSION

5.3.1 PRIMARY EGG MORTALITY

5.3.1.1 THE INCIDENCE OF PREDATION BY VARANIDS

Predation by varanids is the single most important cause of loss of *C. johnstoni* eggs, with annual rates of predation ranging from 21% to 43%. The higher figure is from 1985, where experimental relocation of nests increased their density at Site Three to an unnaturally high level. Also, predation by goannas in 1985 was primarily at the end of incubation, which is atypical when compared to 1983-84. Regardless of these qualifications, the rates of predation by goannas are somewhat lower than those previously reported for this population of *C. johnstoni* (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984), though it should be emphasised that deliberate attempts were made to discourage predation by goannas. However, all rates that have been derived may be inflated due to opening the nests and advertising their presence to the predator, as has been noted for *A. mississippiensis* (Deitz and Hines 1980). This influence cannot account for the losses in 1985 which occurred late in incubation.

There appear to be no intrinsic differences between those clutches which were subsequently taken by goannas soon after laying and those which were not. Whilst the majority of nests taken by goannas were laid in the middle of the nesting season, there is no evidence that those nests have a higher probability of being predated upon.
Crocodylus johnstoni has either never evolved nest guarding behaviours or has evolved and subsequently lost them. It has been argued that this lack is due to the absence of mammalian egg predators in Australia (Webb, Buckworth and Manolis 1983d). However, given the high density at which C. johnstoni nests may be deposited (Chapter 4), it is unlikely that such densities are compatible with nest attendance. For example, while it is possible for six nests to be laid in an area of less than two square metres, it is unlikely that six adult female C. johnstoni could occupy such a space for three months.

On the matter of the nature of predation, it would seem reasonable that the selective pressure for the evolution of nest defence would be more related to the extent of nest predation rather than to the taxonomic grouping of the predator. Surely, a rate of nest loss of between 21% and 45% (this study) or up to 58% (Webb, Buckworth and Manolis 1983d) would provide a significant selective pressure, unless of course there was selection against nest guarding behaviour for some other reason.

Although there are no relevant data available, it should be remembered that the McKinlay River area has a history of perhaps 120,000 years of aboriginal occupation. It is therefore possible that aboriginal hunting of C. johnstoni, or the collection of their eggs, has provided a selection pressure against the maintenance of nesting guarding behaviours.
5.3.1.2 THE INFLUENCE OF EGG SHAPE ON SUBSEQUENT DEVELOPMENT AND ITS RELATIONSHIP TO CLUTCH SIZE

That an egg fails to show signs of development does not necessarily mean that it has not been fertilised. Where such an egg comes from a small clutch of small eggs, none of which exhibit development, then a lack of fertilisation is commonly assumed. Such clutches are almost certainly produced by small, young females, which are believed to have failed to have mated successfully.

However, this simple scheme does not explain the observation that those non-developing eggs from clutches which do show some development are significantly different from those developing eggs. Moreover, those non-developing eggs are statistically the same as eggs from wholly non-developing clutches.

The details of in utero fertilisation have yet to be elucidated in crocodilians (Ferguson 1985; Lance 1987). There is, as yet, no evidence that the occurrence of non-developing eggs in an otherwise normal clutch is a result of lack of fertilisation. Such eggs are often at or near the top of the clutch, indicating that they were among the last eggs laid. Thus it is likely that those eggs occupied the anterior most positions in the oviduct. Such a position could explain the narrow, elongated shape of the egg if space were limiting at such an anterior position. The corollary for wholly non-developing clutches is that in small young females, the maximum width of the oviduct is constrained by the small size of the female, thus producing the elongated eggs characteristic of such clutches. This
scheme may explain the shape of such eggs, but goes no way towards explaining why they should show no signs of developing.

It has been shown that the yolk, with embryo attached, rotates within crocodilian eggs within hours of laying (Webb, Manolis, Whitehead and Dempsey 1986, Webb, Manolis, Dempsey and Whitehead 1987). The rotation apparently depends on the shearing between layers of albumen. Clearly, there is a need to understand more about the dynamics of yolk rotation in crocodilian eggs, especially the possibility that the shape of an egg could inhibit the yolk rotation mechanism.

5.3.1.3 THE INFLUENCE OF EGG ANGLE AND EGG SIZE ON SUBSEQUENT DEVELOPMENT

Neither egg angle within the nest, nor egg weight, proved significant correlates of successful development of viable eggs. These results are hardly surprising as there is no a priori expectation that either should be related to successful development.

The finding that egg size has an intrinsic influence on the probability of successful incubation of Chrysemys picta eggs under laboratory conditions is interesting (Gutzke and Packard 1985). However, given the differences between the carefully structured experiment that detected the effect and the nature of environmental variance in C. johnstoni nests, it is reasonable to expect that if such an effect occurs in C. johnstoni, then it was masked by other variables in the field.
5.3.1.4 THE RELATIONSHIP BETWEEN SEX AND NON-SURVIVAL, AND THE AFFECT OF RELOCATION

The contention of Webb and Smith (1984) that embryos less likely to survive become female is not supported by the simple analysis comparing sex ratios of survivors and non-survivors. A general problem in testing the assertion of Webb and Smith (1984) is a lack of non-surviving embryos. For example, in the simple analysis employed, only 5.2% of animals were non-survivors (see Section 5.2.1.6).

There was no association between the relocation of nests and the survival of embryos. This allows the inclusion of those data in further analyses.

5.3.1.5 FLOODING

As already noted, flooding appears to exert only a minor influence on the survival of *C. johnstoni* embryos. While Webb, Buckworth and Manolis (1983d) and Webb and Smith (1984) have made much of the potential of flooding as a catastrophic agent in embryo survival, there are few data resulting from this study to support such a viewpoint.

Only 2 of 93 clutches examined in 1978-79, none of 28 examined in 1982, and 4 of 119 examined in 1983-85 were flooded (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984; this study). The total for those size years is 6 of 240 clutches (2.5%) lost to
flooding. Webb, Buckworth and Manolis (1983d) report that 12% of located clutches were lost to flooding in 1980. Analysis of long term rainfall records from Darwin indicates that 1979, 1982 and 1983 were effectively average years (Taylor and Tulloch 1985). Both 1978 and 1980 were particularly wet in the late dry season, and this may explain the high occurrence of flooding in 1980.

Irrespective of a catastrophic influence of flooding, lesser affects would accrue from nests being particularly wet. Joanen et al. (1977) found that any submergence in water of a duration greater than two hours induced mortality in at least some A. mississippiensis at any stage of embryonic development: 48 hours submergence killed all eggs. Whitehead (1987a), in examining some of the same nests used in this study, demonstrated that rainfall can markedly alter gas tensions within C. johnstoni nests. Thus, while heavy rains may not lead to catastrophic flooding, temporary inundation and altered gas tensions may result, both of which may compromise the fitness of the embryo.

5.3.2 THE THERMAL ENVIRONMENT OF NESTS, AND ITS RELATION TO THE SEX AND SURVIVAL OF EMBRYOS

5.3.2.1 THE THERMAL ENVIRONMENT OF NESTS

Aspects of the thermal environment of C. johnstoni nests have been noted in previous publications. Temperatures in C. johnstoni nests are certainly very variable in terms of diurnal variation, longer-term seasonal variation, and variation within and between nests (Webb, Buckworth and Manolis 1983d; Webb and Smith 1984). In general,
the temperatures observed and predicted in *C. johnstoni* are more varied than those observed in the nests of other crocodilians (see Magnusson et al. 1985 for review). Moreover it would appear likely that the range of temperatures experienced in *C. johnstoni* nests is as great as that range of temperatures experienced in all other crocodilian nests. Thus, at least from a temperature viewpoint, the nest environment of this crocodile may be the most extreme of all crocodilians.

As the development of the model of nest temperature showed, the variables influencing nest temperature are numerous. However, the most important determinants are seasonal and diurnal cyclical variations, but with additional daily perturbations. Differences between nests in their mean temperature and rate of increase of temperature accounted for only 15% of the total variance in nest temperature: far less than was related to day of laying.

The differences between the results of this study and that of Webb and Smith (1984) in terms of the predictability of *T_h* from *T_1* most likely arise from the differing methodologies. Webb and Smith (1984) did not attempt to model nest temperatures, but rather adjusted observed temperature up or down by a degree depending on the time of day at which the observation was made.

5.3.2.2 NEST TEMPERATURE AND THE SEX OF EMBRYOS

While it has been clearly established that *C. johnstoni* has environmental sex determination, the manner in which environment
determines sex remains unknown, as it does in all other reptiles with environmental sex determination. Temperature is often considered the primary determinant of sex, but the precise role of temperature in sex determination is unclear (Webb and Smith 1984; Webb, Beal, Manolis and Dempsey 1987).

Studies of sex determination in field nests have been limited. Those Ferguson and Joanen (1982, 1983) on *Alligator mississippiensis* primarily demonstrate that there was broad agreement between field and laboratory studies. Similar studies have been carried out on a number of marine and freshwater turtles, but generally with little attention to identifying the environmental correlates of sex (Limpus et al. 1983, 1985; Wilhoft et al. 1983; Bull 1985; Standora and Spotila 1985; Scharzkopf and Brooks 1985; Spotila et al. 1987). Temperature is the most commonly assayed parameter, with both mean temperature and hours spent at particular temperatures being identified as important correlates of sexual phenotype. Generally, the data on mean nest temperature provides a reasonable reflection of laboratory results but, at least in *Chrysemys picta*, it is not the mean but rather the hours spent between the two pivotal temperatures that is important.

The results derived here for the relationship between nest temperature and embryo sex determination both support the importance of mean temperature and also give insights into the discrepancies between laboratory and field incubation. The period of incubation between 20 and 30% of the total incubation time is critical. It is the single most important correlate of embryonic sex. However, the change
in mean temperature in the period 30-50% of incubation and the manner of that change are also important. These results may explain why no constant temperature produces all males: a consistently changing temperature is apparently required after a certain mean temperature has been experienced early in incubation. This interpretation is generally concordant with the results of the *C. johnstoni* shift experiments of Webb, Beal, Manolis and Dempsey (1987). It would thus appear that the production of male *C. johnstoni* is dependent upon a particular temperature trajectory rather than any particular constant temperature.

The influence of substrate type may well reflect differences in the hydric environment of the nests. The hydric environment of embryos with ESD is well known to influence sex determination in other species (Gutzke and Paukstis 1983; Gutzke and Packard 1985, 1986). It is perhaps significant that the hydric environment experienced in the middle trimester of incubation is the most important to embryos of the turtle *Chrysemys picta* (Gutzke and Packard 1986). Also, the thermal and hydric environments can be expected to co-vary (Packard et al. 1985).

5.3.2.3 THE RELATIONSHIP BETWEEN NEST TEMPERATURE AND TOTAL INCUBATION TIME

It has been noted for *C. johnstoni* and *C. porosus* that a change in temperature late in incubation does not drastically alter total incubation time as it does in early incubation (Webb, Beal, Manolis and Dempsey 1987). It has also been suggested that post-
hatchling growth potential is determined at some stage during incubation (Joanen et al. 1987; Webb, Beal, Manolis and Dempsey 1987). The finding that total incubation time is most closely related to mean temperature experienced during 20-30% of total incubation time suggests that at least the pattern of embryological development is largely fixed during this period of incubation. Certainly, this result throws light on why temperature changes late in incubation have little influence on total incubation time. It seems improbable that the period of incubation time most closely related to total incubation time is that which is coincidently most important in terms of sex determination. Thus, there appears as association between sex determination in C. johnstoni and the subsequent physiology of the embryo.

5.3.2.4 THE RELATIONSHIP BETWEEN DAY OF LAYING AND EMBRYONIC SEX

It has already been established that the day on which a clutch is laid will have an important influence on the thermal environment that the embryos will experience. The simple model of sex ratio versus day of laying demonstrates that day of laying, through its influence on temperature, plays a large role in the sex ratio of the resulting hatchlings.

Given that there is a general relationship between female size and day of laying, and also given the relationship stated above, it would appear that there is a general relationship between the size of an adult female and the sex of her offspring. Interestingly, the predicted relationship between day of laying and sex ratio suggests
that the first and last females to lay will tend to produce females, whereas those which lay in the middle of the nesting season produce males. If, as already suggested (Chapter 4), the relationship between size and day of laying is in fact a relationship between female age and day of laying, then it would appear that it is the younger and older females which tend to produce female offspring. Significantly, both these classes of female may be expected to produce a higher than normal proportion of abnormal embryos (Ferguson 1985; Lance 1987), and can be expected to have smaller clutches than middle aged females (Section 4.2.4).

5.3.2.5 THE RELATIONSHIP BETWEEN NEST TEMPERATURE AND EMBRYO SURVIVORSHIP

The modelling of embryonic survival was reasonably simple. However, it was hampered by the lack of non-surviving animals. The three attributes found to be significant were substrate type, depth and hours spent below 28.0°C between 80 and 90% of incubation. All these variables had empirically small effects on survivorship; as survivorship was high in the sample considered, as it generally is when predation by goannas is excluded.

The substrate and depth influences may be expected to relate to the hydric and gaseous environments. As temperatures increase throughout incubation, embryos can be expected to be under increasing metabolic stress, which would amplify any limitations imposed by the hydric and gaseous environments. The influence of hours spent below 28°C is surprising, as it would be expected that little time would be
spent in that temperature range so late in incubation. However, in the sample of nests considered, time spent below 28.0°C during 80-90% of incubation varied between 0 and 65%.

Given that the rate of non-survival with which the model deals is only 12.14%, the influence of any of the above three parameters is understandably minor.

5.3.2.6 THE DETERMINANTS OF HATCHLING SIZE

The determinants of hatchling size considered are without exception those to have been expected. Egg size is known to be correlated with hatchling size in a number of crocodilian species (Ferguson 1985), and is known to be a scaling factor in *C. johnstoni* (Webb, Buckworth and Manolis 1983d; Webb, Beal, Manolis and Dempsey 1987).

The influences of substrate type, temperature and total incubation time are all complex, but at least to some extent agree with laboratory studies. For example, residual yolk weight is negatively correlated with total incubation time and positively correlated with the increase in temperature throughout incubation.

Of the three dimensions examined, head length was by far the least tractable in terms of modelling. The reasons for this are unclear, especially as head length is a good measure of embryonic development in laboratory studies (see for example Webb, Beal, Manolis and Dempsey 1987).
In general, much of the physical makeup of a *C. johnstoni* hatchling is determined by the size of the egg and the environment it experienced as an embryo. Moreover, many of these influences are related, either directly or indirectly, to the time it was laid. For example, the change in mean temperature throughout incubation is largely dependent upon when laying takes place. Also, total incubation time is largely determined during 20-30% of incubation by the temperatures experienced then, and these in turn temperatures are largely determined by day of laying. Thus, the influence of the mother on the size of the offspring is considerable, both in terms of the size of egg she lays and in terms of the environment into which she deposits the egg, and when she deposits them.

5.3.3 HATCHING

The observations of hatching obtained in the study are primarily incidental to the purpose of the study itself. However, that a crocodile may excavate nests of another crocodile, presumably as its own, is rather vexing.

It has already been suggested that the lack of nest defence and attendance in *C. johnstoni* may function to allow high nesting densities. One possible result of this may be a difficulty in a crocodile remaining associated with its nest site, i.e. "remembering" the location of its nest. The observation that a crocodile may excavate a nest that is not its own suggests that this problem may have been overcome.
This intuitively appealing scheme is not without problems. Without invoking group selection arguments, the possible evolutionary histories of such a result are limited. If the above observations prove correct, then altruism appears to be occurring. The most parsimonious explanation of such a result requires a degree of relatedness among the females breeding in such a pool. In particular, it is known that *C. johnstoni* possess a marked homing ability (Webb, Buckworth and Manolis 1983b) and recapture rates in individual pools from year to year are high (Webb, Buckworth and Manolis 1983a). Furthermore, while it is known that neither sex has a tendency to move within the river system more than the other, the overall annual recapture rate for females is higher than for males (42.7% versus 34.21%; unpublished preliminary re-analysis of the data of Webb, Buckworth and Manolis 1983a and Webb et al. unpublished).

The suggestion drawn from these varied observations is that female *C. johnstoni* have a nett tendency to remain and breed in their natal pool or nearby. Thus, within any colonial nesting *C. johnstoni* population, there is a nett tendency for the females to be sufficiently related for kin selection to operate to the extent that the altruism suggested to occur is favoured by selection.
Table 5.1 The fate of 805 eggs from 69 clutches of *C. johnstoni* eggs examined in 1983, 1984 and 1985.

<table>
<thead>
<tr>
<th>Code</th>
<th>Egg fate</th>
<th>1983</th>
<th>1984</th>
<th>1985</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Number</td>
<td>Percent</td>
<td>Number</td>
<td>Percent</td>
</tr>
<tr>
<td>1</td>
<td>Infertile</td>
<td>36</td>
<td>12.41</td>
<td>43</td>
<td>12.57</td>
</tr>
<tr>
<td>2</td>
<td>Egg with laying dents</td>
<td>7</td>
<td>2.41</td>
<td>10</td>
<td>2.92</td>
</tr>
<tr>
<td>3</td>
<td>Probed</td>
<td>16</td>
<td>5.52</td>
<td>12</td>
<td>3.51</td>
</tr>
<tr>
<td>4</td>
<td>Embryonic failure</td>
<td>21</td>
<td>7.24</td>
<td>26</td>
<td>7.60</td>
</tr>
<tr>
<td>5</td>
<td>Drowned</td>
<td>9</td>
<td>3.10</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>6</td>
<td>Dead at/on hatching</td>
<td>8</td>
<td>2.76</td>
<td>1</td>
<td>0.29</td>
</tr>
<tr>
<td>7</td>
<td>Hatched by adult</td>
<td>5</td>
<td>1.72</td>
<td>6</td>
<td>1.75</td>
</tr>
<tr>
<td>8</td>
<td>Hatched - abnormal</td>
<td>12</td>
<td>4.14</td>
<td>5</td>
<td>1.46</td>
</tr>
<tr>
<td>9</td>
<td>Hatched - normal</td>
<td>176</td>
<td>60.69</td>
<td>230</td>
<td>67.25</td>
</tr>
</tbody>
</table>
Table 5.2. Main effect and interaction term coefficients for Year from the modelling of *C. johnstoni* nest temperatures.

<table>
<thead>
<tr>
<th>Year</th>
<th>Main effect</th>
<th>( \ln Day )</th>
<th>MinD</th>
<th>MaxD-1</th>
<th>Day</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>1984</td>
<td>12.8788</td>
<td>2.7439</td>
<td>-0.8082</td>
<td>-0.2907</td>
<td>0.0227</td>
</tr>
<tr>
<td>1985</td>
<td>16.7329</td>
<td>3.5278</td>
<td>-0.2775</td>
<td>-0.5976</td>
<td>-0.0381</td>
</tr>
</tbody>
</table>
Table 5.3. Main effect and interaction term coefficients for the modelling of *C. johnstoni* nest temperature. * indicates that this level of the main effect or interaction term was aliased.

<table>
<thead>
<tr>
<th>Year</th>
<th>Nest</th>
<th>Main</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>1</td>
<td>0.000000</td>
<td>0.000000</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-4.383330</td>
<td>1.453984</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-7.175725</td>
<td>2.298572</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>-0.711108</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-8.194760</td>
<td>2.336970</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>-1.494850</td>
<td>0.816312</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>4.291559</td>
<td>-0.786801</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>-1.624722</td>
<td>0.415189</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>11.275736</td>
<td>-2.778203</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>-0.832930</td>
<td>0.490099</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>-0.760252</td>
<td>0.740361</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>17.900707</td>
<td>-4.361426</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>-0.619395</td>
<td>0.561610</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>9.230508</td>
<td>-2.465182</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>1.382121</td>
<td>-0.322358</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>13.585322</td>
<td>-3.450172</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>10.371128</td>
<td>-2.618666</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>12.354945</td>
<td>-2.987945</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>7.918226</td>
<td>-1.912389</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>1.614477</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>-7.401380</td>
<td>1.657398</td>
</tr>
<tr>
<td></td>
<td>22</td>
<td>-10.852289</td>
<td>3.441894</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>-4.886386</td>
<td>1.289002</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>5.592351</td>
<td>-0.880758</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>3.390458</td>
<td>-0.357382</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>47.801369</td>
<td>-12.821547</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>42.518097</td>
<td>-11.335539</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>6.604899</td>
<td>-1.416187</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>4.746820</td>
<td>-0.984990</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>17.794500</td>
<td>-4.445632</td>
</tr>
<tr>
<td></td>
<td>31</td>
<td>-0.195183</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>32</td>
<td>10.249582</td>
<td>-2.404258</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>78.149216</td>
<td>-19.730124</td>
</tr>
<tr>
<td></td>
<td>34</td>
<td>11.622491</td>
<td>-2.707675</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>12.933638</td>
<td>-2.735827</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>20.556753</td>
<td>-4.567426</td>
</tr>
<tr>
<td></td>
<td>37</td>
<td>14.690923</td>
<td>-3.354193</td>
</tr>
</tbody>
</table>
Table 5.3 Continued. Main effect and interaction term coefficients for the modelling of *C. johnstoni* nest temperature. * indicates that this level of the main effect or interaction term was aliased

<table>
<thead>
<tr>
<th>Year</th>
<th>Nest</th>
<th>Main</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>1</td>
<td>-3.161369</td>
<td>1.755149</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-3.951220</td>
<td>2.218661</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.559394</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>-6.572486</td>
<td>1.957317</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-6.187843</td>
<td>2.198989</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>0.617672</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>-5.637695</td>
<td>2.131834</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>-3.527574</td>
<td>1.441590</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>1.113383</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>-3.715199</td>
<td>1.845881</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>-9.059411</td>
<td>2.840138</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>-3.254280</td>
<td>1.746348</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>-5.628491</td>
<td>1.947610</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>0.687757</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>3.932888</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>-3.759763</td>
<td>1.906103</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>2.233938</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>6.933473</td>
<td>-1.747386</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>3.290501</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>6.502300</td>
<td>-1.284279</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>2.831430</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>22</td>
<td>6.387239</td>
<td>-0.573219</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>-4.888162</td>
<td>2.216168</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>3.641441</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>-2.535818</td>
<td>1.585500</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>2.632073</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>2.149526</td>
<td>0.209971</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>-2.267496</td>
<td>1.487929</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>-9.100369</td>
<td>3.378122</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>4.972289</td>
<td>-0.578302</td>
</tr>
<tr>
<td></td>
<td>31</td>
<td>-0.928466</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>32</td>
<td>-5.798051</td>
<td>2.633514</td>
</tr>
<tr>
<td></td>
<td>33</td>
<td>-0.874722</td>
<td>0.895290</td>
</tr>
<tr>
<td></td>
<td>34</td>
<td>10.732541</td>
<td>-1.821338</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>8.907796</td>
<td>-1.442941</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>-4.176970</td>
<td>1.802806</td>
</tr>
<tr>
<td></td>
<td>37</td>
<td>-5.461480</td>
<td>2.138828</td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>3.226259</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td>2.446028</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>41</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>42</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>43</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>44</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>45</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>46</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>47</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>48</td>
<td></td>
<td>*</td>
</tr>
</tbody>
</table>
Table 5.3 Continued. Main effect and interaction term coefficients for the modelling of *C. johnstoni* nest temperature. * indicates that this level of the main effect or interaction term was aliased

<table>
<thead>
<tr>
<th>Year</th>
<th>Nest</th>
<th>Main</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>1</td>
<td>-7.587888</td>
<td>1.396045</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-7.269968</td>
<td>1.947270</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-2.494635</td>
<td>0.683438</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>-8.633347</td>
<td>2.043586</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-3.696768</td>
<td>0.899874</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>-0.160696</td>
<td>0.104969</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>-4.910040</td>
<td>1.278225</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>-2.262285</td>
<td>0.463468</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>-12.161507</td>
<td>2.806312</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>-6.014448</td>
<td>0.929100</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>-7.053073</td>
<td>1.298285</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>-8.251665</td>
<td>1.695814</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>-5.042789</td>
<td>1.424721</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>-8.332101</td>
<td>1.683074</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>-5.080304</td>
<td>0.866449</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>-3.318735</td>
<td>0.496862</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>-1.870153</td>
<td>0.051524</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>-0.709006</td>
<td>-0.118769</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>-3.426534</td>
<td>1.107631</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>-5.623162</td>
<td>1.284620</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>-10.842571</td>
<td>2.217726</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>-4.397011</td>
<td>0.748838</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>-4.870099</td>
<td>1.091627</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>-7.169477</td>
<td>1.647287</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>-7.243593</td>
<td>1.548305</td>
</tr>
<tr>
<td></td>
<td>28</td>
<td>-5.200560</td>
<td>1.255944</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>
Table 5.4. Predicted sex ratio (proportion male) cross classified by the increase in mean temperature between 20-30\% and 30-40\% of incubation ($\Delta t_{20-40}$) and between 30-40\% and 40-50\% of incubation ($\Delta t_{30-50}$). * indicates that the combination of temperature changes did not occur in the sample of nests examined.

<table>
<thead>
<tr>
<th></th>
<th>$\Delta t_{30-50}$</th>
<th>0.30</th>
<th>0.71</th>
<th>1.04</th>
<th>1.34</th>
<th>1.80</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Delta t_{20-40}$</td>
<td>0.54</td>
<td>0.04849</td>
<td>1.17874</td>
<td>0.83919</td>
<td>0.13595</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.91</td>
<td>0.16286</td>
<td>0.15396</td>
<td>0.99869</td>
<td>0.00268</td>
<td>0.32236</td>
</tr>
<tr>
<td></td>
<td>1.56</td>
<td>0.45366</td>
<td>0.06513</td>
<td>0.43360</td>
<td>0.07389</td>
<td>0.01330</td>
</tr>
</tbody>
</table>
Table 5.5. Predicted influence of substrate type on survivorship of *C. johnstoni* embryos.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Survivorship ± Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine sand</td>
<td>0.9764 ± 0.0300</td>
</tr>
<tr>
<td>Medium/fine sand</td>
<td>0.9812 ± 0.0231</td>
</tr>
<tr>
<td>Medium sand</td>
<td>0.9789 ± 0.0232</td>
</tr>
<tr>
<td>Medium/coarse sand</td>
<td>0.9711 ± 0.0314</td>
</tr>
<tr>
<td>Coarse sand</td>
<td>0.8188 ± 0.0932</td>
</tr>
<tr>
<td>Fine sand/humus</td>
<td>0.9999 ± 0.0000</td>
</tr>
<tr>
<td>Sand/clay</td>
<td>0.8163 ± 0.1910</td>
</tr>
</tbody>
</table>
Table 5.6. Main effect and interaction term coefficients for the influence of substrate type on *C. johnstoni* residual yolk weight. * indicates that this level of the main effect or interaction was aliased.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Main effect</th>
<th>Incubation time</th>
<th>Egg weight</th>
<th>Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine sand</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>Medium/fine sand</td>
<td>-3.9528</td>
<td>0.0044</td>
<td>0.0391</td>
<td>0.0675</td>
</tr>
<tr>
<td>Medium sand</td>
<td>1.7924</td>
<td>-0.1615</td>
<td>0.2040</td>
<td>-0.0980</td>
</tr>
<tr>
<td>Medium/coarse sand</td>
<td>1.5517</td>
<td>-0.2003</td>
<td>0.2182</td>
<td>0.0223</td>
</tr>
<tr>
<td>Coarse sand</td>
<td>-77.7127</td>
<td>0.9332</td>
<td>0.0375</td>
<td>0.1803</td>
</tr>
<tr>
<td>Fine sand/humus</td>
<td>26.4660</td>
<td>-0.2027</td>
<td>-0.0629</td>
<td>-0.0441</td>
</tr>
<tr>
<td>Sand/clay</td>
<td>17.6987</td>
<td>*</td>
<td>0.2608</td>
<td>-1.4837</td>
</tr>
</tbody>
</table>
Table 5.7. Main effect and interaction term coefficients for the influence of substrate type on C. *johnstoni* hatchling yolk-free weight. * indicates that this level of the main effect or interaction was aliased.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Main effect</th>
<th>Incubation time</th>
<th>ΔT</th>
<th>ln ΔT</th>
<th>Depth</th>
<th>Egg weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine sand</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>Medium/fine sand</td>
<td>-55.6840</td>
<td>0.6703</td>
<td>-3.4642</td>
<td>6.3194</td>
<td>-0.1754</td>
<td>0.1549</td>
</tr>
<tr>
<td>Medium sand</td>
<td>-50.8790</td>
<td>0.6793</td>
<td>-3.3505</td>
<td>8.7457</td>
<td>-0.2340</td>
<td>0.0067</td>
</tr>
<tr>
<td>Medium/coarse sand</td>
<td>-79.7040</td>
<td>1.0476</td>
<td>-7.1405</td>
<td>21.6709</td>
<td>-0.1664</td>
<td>-0.0060</td>
</tr>
<tr>
<td>Coarse sand</td>
<td>86.2859</td>
<td>-1.1380</td>
<td>-0.1550</td>
<td>*</td>
<td>-0.9988</td>
<td>0.2767</td>
</tr>
<tr>
<td>Fine sand/humus</td>
<td>254.2257</td>
<td>-0.0106</td>
<td>104.1887</td>
<td>-486.8546</td>
<td>-0.43767</td>
<td>0.1180</td>
</tr>
<tr>
<td>Sand/clay</td>
<td>77.4135</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>2.6817</td>
<td>-1.8263</td>
</tr>
</tbody>
</table>
Table 5.8. Main effect and interaction term coefficients for the influence of substrate type on *C. johnstoni* hatchling head length. * indicates that this level of the main effect or interaction was aliased.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Main effect</th>
<th>( \ln ) Incubation time</th>
<th>( \Delta T )</th>
<th>( \ln \Delta T )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine sand</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>Medium/fine sand</td>
<td>-6.7096</td>
<td>1.5663</td>
<td>-0.0053</td>
<td>-0.1014</td>
</tr>
<tr>
<td>Medium sand</td>
<td>-7.3062</td>
<td>1.6586</td>
<td>0.0167</td>
<td>-0.0699</td>
</tr>
<tr>
<td>Medium/coarse sand</td>
<td>-8.9096</td>
<td>2.0190</td>
<td>-0.1143</td>
<td>0.3979</td>
</tr>
<tr>
<td>Coarse sand</td>
<td>3.8170</td>
<td>-0.8963</td>
<td>0.0135</td>
<td>*</td>
</tr>
<tr>
<td>Fine sand/humus</td>
<td>2.7755</td>
<td>0.3079</td>
<td>2.0735</td>
<td>-9.0760</td>
</tr>
<tr>
<td>Sand/clay</td>
<td>-0.3682</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>
Fig. 5.1. The incidence of predation of *C. johnstoni* nests by *Varanus gouldii* with respect to the time since laying.
Fig. 5.2. The relationship between the cumulative number of *C. johnstoni* nests taken by *Varanus gouldii* and the cumulative number of nests laid in 1983 (b) and 1984 (a).
Cumulative number of clutches taken by goannas

Cumulative number of clutches laid

(a)

(b)
Fig. 5.3. Observed temperatures in 104 *C. johnstoni* nests in the period 1983-85, with respect to the day on which the observation was made. Open circles represent a coincidence of data points.
Fig. 5.4. Predicted temperatures in three *C. johnstoni* nests: one each from 1983 (thin line), 1984 (dotted line) and 1985 (thick line). The lines extend from the observed laying date to the observed hatching date for each clutch.
Fig. 5.5. The relationship between total incubation time and sex ratio in *C. johnstoni*. Open squares are data from Webb, Beal, Manolis and Dempsey (1987) and closed circles are data from this study. Numbers represent sample sizes. Open circles in open squares represent a coincidence of data points.
A scatter plot showing sex ratio (proportion males) against total incubation time (days). The x-axis represents total incubation time in days, ranging from 60 to 130. The y-axis represents sex ratio, ranging from 0 to 1.00. The data points are organized into clusters, suggesting a relationship between incubation time and sex ratio. Numbers indicate the count of data points at each location.
Fig. 5.6. The $\chi^2$ for fitting mean temperature (a), the square of mean temperature (b) and the percentage of time spent between 31°C and 33°C (c) against hatchling sex ratio for incubation time divided into 10% sections.
Incubation complete (o/o)

(a) 

(b) 

(c) 

Incubation complete (%)
Fig. 5.7. The predicted relationship between hatchling sex ratio and the mean temperature experienced in the period 20-30% of incubation.
Sex ratio (proportion male)

Temperature (°C)
Fig. 5.8. The predicted relationship between sex ratio and the change in mean temperature between 20-30% and 30-40% of incubation (Δt20-40) and between 30-40% and 40-50% of incubation (Δt30-50). Shown are Δt30-50’s of (a) 0.30°C, (b) 0.71°C, (c) 1.04°C, (d) 1.34°C and (e) 1.80°C.
Fig. 5.9. The relationship between observed total incubation time among 49 *C. johnstoni* nests and the predicted mean temperature throughout incubation. Open circles represent a coincidence of data points.
Fig. 5.10. The relationship between observed total incubation time among 49 *C. johnstoni* nests and the predicted mean temperature during the period 20-30% of incubation. Open circles represent a coincidence of data points.
Fig. 5.11. The predicted relationship between the day of laying of *C. johnstoni* clutches in 1983-1985 and the sex ratio of the hatchlings.
Fig. 5.12. The predicted relationship between egg depth and the probability of embryonic survival.
1.00
0.98
0.96
0.94
0.92
0.90
0.90
10
20
30
40
Egg depth (cm)

Probability of survival
Fig. 5.13. The predicted relationship between the proportion of time that *C. johnstoni* embryos spent below 28°C during 80-90% of incubation and their probability of survival.
CHAPTER 6

SHORT-TERM SURVIVAL AND GROWTH OF HATCHLINGS

6.1 INTRODUCTION

The incubation environment experienced by C. johnstoni eggs plays a fundamental role in determining the future of embryos. It determines their sex and, to an extent, their physical dimensions (Chapter 5). Also, it has been shown that the day on which a nest is laid has a major influence on those parameters. However, does the nest environment determine or in any way influence the probability of survival of those hatchlings, and their pattern of post-hatchling growth?

Ferguson and Joanen (1982, 1983) in their studies of environmental sex determination in Alligator mississippiensis maintained hatchlings from laboratory incubated eggs under controlled conditions to one year of age. They found that egg incubation environment did influence hatchling size and post-hatching growth to one year of age. Unfortunately, the results of that experiment are difficult to refer to a natural situation, since that would require the assumption that the patterns of mortality in the field and under controlled conditions are identical. Additionally, the sample size for that experiment was very low (N = 12). Further and more extensive studies of A. mississippiensis have shown that growth and survival to 18 months of age are indeed under the influence of incubation conditions (Joanen et al. 1987).
Garnett and Murray (1986) in a study of *C. porosus* hatchling growth under controlled conditions identified an effect which may have been attributable to incubation environment. Unfortunately, each clutch of eggs considered came from a different environment, and hence a genetical clutch effect could not be ruled out. As in the case of the studies of Ferguson and Joanen, Garnett and Murray (1986) raised the animals under controlled conditions, and hence the application to the field of those results is dependent upon the assumption of identical patterns of survival. A limited study of *C. johnstoni* by Webb, Buckworth and Manolis (1983c) failed to detect any difference attributable to incubation environment in the general pattern of growth and survival of hatchlings to one year of age. However, they did note that under raising conditions of low crocodile density, females tended to survive more commonly than did males.

Packard et al. (1981, 1983) considered hatchling condition in two species of freshwater turtles. On basis of the results of Swingland and Coe (1979), that larger hatchlings of the giant tortoise (*Geochelone gigantea*) had a higher rate of survival to one year of age than did smaller hatchlings, Packard et al. (1981, 1983) suggested that hatchling size in *Chelydra serpentina* and *Chrysemys picta* was similarly related to survival. The analysis of Swingland and Coe (1979), however, is perhaps over-simple, and on this basis it may be incautious to accept their findings about the nature of the relationship between hatchling size and survival.

That larger hatchlings can have a higher probability of survival is also reported for the lizards *Uta stansburiana* and
Sceloporus undulatus (Ferguson and Bohlen 1978, Fox 1978, Ferguson et al. 1982), but again the real relationship between hatchling size and survival may not be as simple as their analysis suggests. Fox (1975, 1978, 1983) demonstrated the action of natural selection on the morphological and behavioural phenotypes of U. stansburiana and has shown that the extent and nature of selection varies between years (Fox 1978). In particular, the survival advantage of large size has been shown to vary both within and between years (Ferguson and Bohlen 1978, Fox 1978, Ferguson et al. 1982, Ferguson and Fox 1984).

This Chapter considers the short-term survival and growth of C. johnstoni hatchlings under natural conditions in two different years. The experiment was structured such that all hatchlings at the seven major study Sites were collected at or near the point of hatching, and then released into the pool at Site One. Some period of time after the last hatching was released, all hatchlings surviving in the pool were recaptured and the patterns of survival and growth examined.

6.2 METHODS

6.2.1 NUMBER AND SOURCES OF ANIMALS RELEASED

In 1984, 246 hatchlings were used in this experiment. Of those, 210 were collected directly from 26 nests at the point of hatching (Chapter 5) and 36 were captured from pools less than 48 hours after having been released from the nest by an adult crocodile. In 1985, 139 hatchlings were used, 113 coming directly from 13 nests.
and 26 retrieved from pools. All animals were individually marked, weighed, measured, and sexed before release at Site One (Chapter 3) within 24 hours of being collected. Residual yolk weight was estimated using the method of Smith and Webb (1987, Appendix 2).

In 1984, the first release took place on 28 October and the last on 23 November. In 1985, the first release took place on 1 November and the last on 22 November.

6.2.2 RECAPTURE OF HATCHLINGS

On 1 December 1984 and 31 November 1985, seven days after the last release, an intensive attempt was made to recapture all hatchlings which had been previously released. Capture was by hand, using torches to locate the hatchlings by eyeshine. The pool was constantly scanned with a powerful spotlight and the capture effort continued until no eyeshine which could not be accounted for, was observed in the pool for a period of 30 minutes. Additional to scanning the pool itself, the banks of the pool and the creek system at the eastern end of the pool were also scanned with a spotlight. Further to the pool and its immediate surrounds, all associated water bodies within 1 km were checked with torches for the presence of hatchlings. The recapture took 17 people 10 hours in 1984 and 18 people 9 hours in 1985. All hatchlings recaptured were weighed, measured and sexed within 48 hours of recapture.
6.2.3 CAPTURE AND STOMACH PUMPING OF LARGER CROCODILES

In both 1984 and 1985, a sample of non-hatchling *C. johnstoni* was collected for stomach contents analysis. Capture was generally effected using fine nets (Webb and Messel 1977) except in a few cases where yearling crocodiles were captured by hand.

Stomach contents were obtained using the method of Webb, Manolis and Buckworth (1982) with larger crocodiles being immobilised with Gallamine triethiodide (Loveridge and Blake 1972; Woodford 1972) prior to stomach pumping. The stomach contents were stored in 70% alcohol until being examined under a dissecting microscope.

6.3 RESULTS

6.3.1 DIMENSIONS AND CHARACTERISTICS OF HATCHLINGS RELEASED

Of the 246 hatchlings released in 1984, 49 were male and 197 were female, giving a sex ratio of 0.20. In 1985, 62 of the 139 hatchlings released were male, giving a sex ratio of 0.45. The mean head length, snout-vent length, trunk length, total weight, estimated residual yolk weight and yolk-free weight of the two samples appear in Table 6.1.

The sex of the animals is disregarded in the analysis of their dimensions, as sex is simply a correlate of incubation environment which itself directly determines the dimensions in conjunction with egg parameters (Chapter 5).
The hatchlings released in 1984 were significantly larger than those released in 1985 in all measures except head length. Additionally, the animals released in 1984 were significantly more variable in three of the measures (Table 6.1). Mean days exposure (the average number of days between release and the termination of the experiment) was significantly greater in 1984 than in 1985, although the variance was not.

6.3.2 RELATIONSHIP BETWEEN DAY OF RELEASE AND THE PHYSICAL CHARACTERISTICS OF HATCHLINGS

Given that the day on which the hatchlings were released, and hence the number of days they were exposed to risk in the experiment, is a reflection of the day of hatch, and hence total incubation time (Chapters 4 and 5), it is possible that the size of the animals released varied significantly throughout the experiment. Therefore, simple linear regression was used to examine variation in dimensions throughout the period of release.

In 1984, hatchling weight, residual yolk weight and yolk-free weight were found to vary significantly with day of release. Residual yolk weight decreased significantly with day of release \( (F_{1,244} = 5.95; 0.05 > P > 0.01) \), while hatchling weight and yolk-free weight increased significantly \( (F_{1,244} = 7.90; 0.01 > P > 0.001 \) and \( F_{1,244} = 25.84; 0.001 > P, \) respectively). In 1985, none of the parameters measured varied significantly with day of release.
6.3.3 DIMENSIONS AND CHARACTERISTICS OF HATCHLINGS RECAPTURED

In 1984, 110 hatchlings were recaptured, and a further three were known to be present in the pool but avoided capture. No hatchlings were located outside the pool itself and a repeat survey of the pool two days later failed to detect any hatchlings other than the three uncaught individuals. Additional to the 110 hatchlings recaptured, 10 unmarked individuals were captured for the first time, and must have resulted from a nest previously undetected at that pool. Those individuals will not be considered in the following analysis.

If the three individuals which were not recaptured in 1984 are considered to have been animals released as part of the experiment, then the survival rate for the experiment is 46% over a mean exposure in the experiment of 19.9 days. Of the 110 individuals recaptured, 28 were male and 82 were female, giving a sex ratio of 0.25. The difference in sex ratio from those released to those recaptured (0.20 to 0.25) was not quite significant ($\chi^2 = 3.82, 0.10 > P > 0.05$). The mean dimensions of the two samples of animals recaptured appear in Table 6.2.

In 1985, 65 hatchlings were recaptured and one individual could not be recaptured. As in 1984, no hatchlings were located outside the pool itself. If the one hatchling not recaptured is considered to have been released as part of the experiment, the survival rate is 47% over a mean exposure of 18.8 days. Of the 65 recaptured, 24 were male and 41 were female, giving a sex ratio of 0.37. Again, the shift in sex ratio from those released to those
recaptured (0.47 to 0.37) was not quite significant ($\chi^2 = 2.92, 0.10 > P > 0.05$).

In 1984 survival was biased against females whereas in 1985 survival was biased against males, though neither difference was statistically significant. If the two samples are treated as one, the sex ratio of all animals released is 0.29 and that of all animals recaptured is 0.30 with survival for both years considered together appearing to be independent of sex ($\chi^2 = 0.12, 0.90 > P > 0.50$). When the rate of survival, independent of sex, in the two years is compared, no significant difference can be found ($\chi^2 = 0.0561, 0.50 > P > 0.10$).

The pattern of differences that existed between the samples released in 1984 and 1985 was maintained to a large extent among those animals recaptured. The animals recaptured in 1984 were significantly larger than animals recaptured in 1985 in snout-vent length, trunk length, weight, residual yolk weight and yolk free weight, as indeed they were at the point of release. However, the mean number of days spent in the experiment was different in each year. In 1984, the mean exposure of animals recaptured was greater than that of all animals released (21.58 versus 19.94), whereas those recaptured in 1985 had a mean exposure less than that of all animals released (14.66 versus 18.84) (Tables 6.1 and 6.2).
6.3.4 EVIDENCE FOR THE ACTION OF NATURAL SELECTION

An examination of the dimensions at hatching of survivors and non-survivors was carried out to determine if natural selection was operating on the phenotype of the hatchlings. The expectation is that the variance in the characteristics measured at hatching should be greater in the non-survivors than in the survivors, indicating the action of natural selection in removing variation from the population (Fox 1975, 1978). Additionally, any difference in the mean for a particular variable between survivors and non-survivors may indicate the action of directional selection (Fox 1975, 1978).

Given that it has been shown that the nature and extent of natural selection on the lizards *U. stansburiana* and *S. undulatus* varies within and between years (Ferguson and Bohlen 1978, Fox 1978, Ferguson et al. 1982, Ferguson and Fox 1984) the data sets for 1984 and 1985 will at this point be treated separately.

The evidence for stabilising selection in the data for 1984 is quite strong (Table 6.3). The variance in head length (Fig. 6.1), snout-vent length, trunk length, total weight and yolk-free weight was significantly greater among non-survivors than survivors. Some suggestion of directional selection is apparent in a marginally significant difference in mean head length between survivors and non-survivors, with survivors having a slightly larger head length at hatching than did non-survivors (3.75 cm versus 3.72 cm). It is, however, difficult to ascribe biological meaning to such a minor shift in mean size (0.03 cm or 0.8% of initial mean head length).
Among the animals from 1985, the evidence for stabilising selection is far less strong (Table 6.4). Of the available measures, only head length provided any indication of the action of stabilising selection (Fig. 6.2). It is interesting to note that it was head length that showed the strongest evidence for the action of selection in 1984. There was no significant indication of directional selection in this character in 1985.

6.3.5 ANALYSIS OF HATCHLING SURVIVAL

As has already been noted, in studies of the survival of other reptiles, the extent and nature of selection may vary within and between seasons. There is, therefore, no a priori expectation that selection should or should not be the same in 1984 and 1985.

We have seen that total survivorship was the same in both years and that the possibility of stabilising selection on head length was observed. That the action of stabilising selection was identified in additional parameters in 1984 compared to 1985 is probably simply a reflection of the fact that the variance in those parameters was greater in 1984 (Tables 6.1 - 6.4). Thus, it would appear that the extent of selection was similar in the two years.

When the distribution of survivors and non-survivors is plotted against days exposure, i.e. days between release and recapture (Figs. 6.3 and 6.4), there is evidence for a difference in the pattern of survival between the two years. In 1984 (Fig. 6.3) those individuals exposed for the shortest and longest times suffered the
greatest mortality, whereas those at liberty for an intermediate time enjoyed highest survivorship. The situation in 1985 is clearly different (Fig. 6.4). Here, those individuals at liberty longest apparently suffered the highest mortality, whereas those released last enjoyed much higher survivorship. In 1984, the range of exposures related to surviving hatchlings was 12 - 34 days, whereas in 1985 it was 8 - 26 days.

It is not easy to interpret this difference biologically. Though it is known that some hatchlings survived 34 days in 1984 and 26 days in 1985, it is unknown precisely when hatchlings died. From observation, hatchlings in the wild are most easy to catch within 24 hours of hatching, and after that become more wary and adept at escape. Thus, it is possible, indeed highly likely, that the majority of mortality occurred within hours of release. Alternatively, mortality could be entirely random, although the evidence for stabilising selection would argue against this.

The data on hatchling survival are presented in a different manner in Fig 6.5, which plots the cumulative number of hatchlings which survived against the cumulative number of hatchlings released for both 1984 and 1985. The patterns in the two years are again different. In 1984, there is an effectively linear relationship between the number of survivors and the number released throughout most of the experiment, though the final three points suggest that the probability of survival declined at the end of the experiment. The pattern in 1985 appear to be different in that a single relationship was evident in which the probability of survival tended to increase as the experiment progressed.
From these facts, there is some indication that the dynamics of survival are different in the two years. Broadly, the pattern of survival and non-survival in 1984 appears generally independent of time, whereas in 1985 it seems to an extent time dependent. This provides additional support for the contention that the pattern but not the extent of selection varied between the two years.

Given clearly established differences between the two years, they will be further considered separately. Logistic regression analysis was used to analyse the pattern of survival in each year. The available measures of size, included as linear, square and ln terms, were tested in the regression. Of those available, only head length was significant ($X^2_1 = 17.210, 0.005 > P$). When the fitted values of this model were examined it correctly predicted 56.12% of individuals (those animals with a fitted survivorship of $> 0.50$ are considered survivors). While this may appear a good fit, it has already been shown that of the parameters of size considered, head length is the least tractable in terms of modelling. Thus, while there is a clear association between head length and survival, there is no obvious biological basis for why this is so.

Given the apparent lack of usefulness of hatchling size as a predictor of survivorship, to determine whether it is possible to predict hatchling survivorship, the incubation environment was examined. In particular, the mean temperatures predicted for 10% periods of incubation (Chapter 5) were considered in this context. Each term was added as a three level factor after the parabolic and linear terms of head length had been fitted to the model.
Only one of the periods of mean temperature was found to be significant, and that was for the period of 80-90% of incubation ($\chi^2 = 10.787, 0.005 > P$). This model correctly identified 67.3% of individuals as survivors and non-survivors. The predicted relationship between head length and survival appears in Fig. 6.6 and that for temperature in Table 6.5.

The modelling of survival in 1985 was approached in the same manner. After the inclusion of head length, mean nest temperature in two of the 10% periods were found to be significant. They were for the period 0-10% of incubation ($\chi^2 = 17.505, 0.005 > P$) and 60-70% of incubation ($\chi^2 = 13.549, 0.005 > P$). This model correctly identified 77.5% of individuals as survivors and non-survivors. The predicted relationship between head length and survival appears in Fig. 6.7 and those between temperature and survival in Tables 6.6 and 6.7. As is obvious in Fig. 6.7, the relationship between head length and probability of survival is effectively linear. By using the measures of nest temperature in the analysis, a number of hatchlings were excluded from the analysis. This exclusion rendered the pattern of stabilising selection on head length non-significant.

The differences between the results of the modelling of hatchling survival in the two years is largely explained by the differences in the thermal regimes of those years (Table 6.8). In 1984, it was the temperature in 80-90% of incubation that was related to hatchling survival. Table 6.5 indicates that there was a survival advantage related to intermediate and high temperatures in 1984. The mean and variance of nest temperatures during that period were higher
in 1985 than in 1984, and the mean temperature in 1985 was far closer to the apparent optimum than it was in 1984 (compare Tables 6.5 and 6.8). Thus, circumstances may not have existed in 1985 to constrain hatchling survival. The variance in temperature was significantly greater during that period in 1984 than in 1985 ($F_{16,12} = 6.31$, $0.01 > P > 0.002$).

In 1985 there were survival advantages related to low temperatures in the 0-10% period (Table 6.6) and with higher temperatures in the 60-70% period (Table 6.7). The temperatures were lower during the 0-10% period in 1984 than in 1985 and again the temperatures in 1984 may not have been such as to constrain survivorship. The pattern in the 60-70% period is somewhat different. It would be expected that temperatures during this period should be higher in 1984 than in 1985, but this is not the case. However, the variance is significantly greater in 1984 than in 1985 ($F_{17,12} = 3.42$, $0.05 > P > 0.02$). It is of course possible, that temperatures in that period in 1984 did not reach levels that would have offered any survival advantage.

The contention that there is an association between large size and hatchling survival was tested with head length, snout-vent length, hatchling total weight, residual yolk weight hatchling yolk-free weight. In all cases, individuals were identified by a factor describing those with a value greater than, or equal, to the mean for that parameter, or less than the mean for that parameter. The factor was then tested in the regression model by itself. In the case of head length, it proved was marginally significant ($\chi^2_1 = 4.158$, $0.05 > P$
None of the other measures reached significance, with \( \chi^2 \) values between 0.017 and 1.857. Thus, there is no apparent survival advantage in large size, and the single significance of head length implies that head length is reflecting something other than size.

### 6.3.6 ANALYSIS OF HATCHLING GROWTH

Over the limited lifespan of this experiment, hatchling growth could be assumed to be minimal. However, among those that survived, the pattern of growth could be affected by the incubation environment. The change in hatchling dimensions through the experiment in 1984 and 1985 appears in Table 6.9. The hatchlings used in the 1985 experiment grew significantly less than the 1984 animals in terms of head length, snout-vent length and trunk length, and lost less weight (Table 6.9). The change in dimensions was equally variable in the two years. In the analysis of growth, only trunk length and weight will be considered, as head length and snout-vent length are sensitive to the very rapid changes in head length that occur immediately after hatching, which represent allometric changes in the skull after having its development constrained by being in the egg.

Weight at recapture was initially examined using a model which considered weight at release, days between release and recapture, residual yolk weight, yolk-free weight, total incubation time and sex. Of these, weight at release was the most important predictor of weight at recapture and accounted for 80% of the total variance in weight at recapture \( (F_{1,153} = 1033.59, \ 0.005 > P) \). Days exposure also accounted for a significant portion of the total
variance (8%, $F_{1,153} = 101.35$, 0.005 $> P$) as did year (0.5%, $F_{1,153} = 5.76$). The coefficient for year in the model indicates that in 1985, the animals lost 0.78 g more weight than they did in 1984. The total model accounted for 88% of the total variance in hatchling weight at recapture. The predictive relationship was:

$$\text{Weight at recapture} = 1.13 + 0.93 \times (\text{Weight at release}) - 0.15 \times (\text{Days}) - 0.78 \times (\text{Year})$$

\text{Eq. 6.1}

In the analysis of trunk length growth, trunk length at release was the most important variable; however, the model was more complex than that for the change in weight. Trunk length at release accounted for 54% of the total variance in trunk length at recapture ($F_{1,151} = 322.56$, 0.005 $> P$). The next most important predictor of hatchling trunk length at recapture was total hatchling weight at release which accounted for 10% of the total variance ($F_{1,151} = 60.01$, 0.005 $> P$), followed by days exposure accounting for 8% of the total variance ($F_{1,151} = 47.56$, 0.005 $> P$). Additional significant variables are year accounting for 1.3% of the total variance ($F_{1,151} = 7.79$, 0.01 $> P > 0.001$) and hatchling yolk-free weight at release accounting for 0.7% of the total variance ($F_{1,151} = 4.33$, 0.05 $> P > 0.01$). The complete model accounted for 74% of the total variance in trunk length at recapture. The predictive relationship was:

$$\text{Trunk length} = 3.42 + 0.32 \times (\text{Trunk length at release}) + 0.03 \times (\text{Hatchling weight at release}) + 0.014 \times (\text{Days}) + 0.12 \times (\text{Year}) + 0.02 \times (\text{Yolk-free weight at release})$$

\text{Eq. 6.2}
6.3.7 STOMACH CONTENTS OF LARGER CROCODILES

In 1984, seven non-hatchling crocodiles were captured in the pool. Their sizes ranged from 0.55 m total length to 1.89 m total length. The remains of hatchlings were located in the stomachs of five of the animals, all of which were greater than 1 m total length. The seven animals examined represented approximately half the total number of non-hatchlings in the pool.

In 1985, seven non-hatchling crocodiles were recovered from the pool, and unlike 1984, these seven animals represented all the non-hatchling crocodiles in the pool. They ranged from 0.7 m total length to 1.73 m total length. Of the seven, only one crocodile (1.17 m total length) had the remains of a hatchling in its stomach.

6.4 DISCUSSION

6.4.1 EXTENT AND CAUSES OF MORTALITY

_Crocodylus johnstoni_ in the McKinlay River area has been estimated to exhibit a survival rate of between 7% and 17% from hatching to one year of age (Smith and Webb 1985). This is a relatively low rate of survival when compared to _C. porosus_ with 54% (Webb, Manolis, Whitehead and Letts 1984) and _A. mississippiensis_ with 35% (Nichols et al. 1976). That hatchlings of _C. johnstoni_ should exhibit approximately the same rate survival under similar conditions in the wild in two different years is not expected, and may well be fortuitous.
The causes of mortality of *C. johnstoni* hatchlings are largely unknown. From this study, it is apparent that cannibalism is one source of mortality and that it is variable in extent. Unfortunately, the extent of hatchling loss attributable to cannibalism is unknown in any crocodilian species.

Additional to cannibalism, predation is likely to be the major source of hatchling loss. Unfortunately, there are few available data on the predators of *C. johnstoni* hatchlings or those of other species. Freshwater turtles and birds are likely to be major predators.

### 6.4.2 THE ACTION OF NATURAL SELECTION

The action of natural selection in the survival of crocodilian hatchlings is documented here for the first time. Survival is clearly not random, and the nature of the selection operating is primarily stabilising. This contrasts completely with the data of Swingland and Coe (1979) that larger hatchlings of *Geochelone gigantea* survived better than did smaller ones, which implies strongly directional selection for larger hatchling size. However, in that study, Swingland and Coe (1979) simply compared sample hatchlings from the 50 largest and 50 smallest eggs at each of two sites, and then examined the number of resulting hatchlings which survived to one year of age. For this type of comparison to be valid, the distribution of egg sizes should be strictly normal and the probability of survival be strictly related to hatchling size. As we have seen, if the sample of *C. johnstoni* hatchlings used in 1984 and 1985 are divided into two
groups on the basis of whether they were less than the mean or equal to and/or greater than the mean for a series of parameters, there is no suggestion that larger animals survive better than smaller animals. The one exception to this generality is, of course, head length.

Stabilising selection did not apparently occur on all aspects of size in both years (Tables 6.3 and 6.4). Head length, snout-vent length, trunk length, yolk-free weight and total weight showed the action of stabilising selection in 1984. In 1985, only head length showed evidence of the action of stabilising selection.

There is no a priori reason for head length to be the object of selection. If the major cause of hatchling loss is predation, one would expect that the overall size of the hatchling to be correlated with the survival of the animal. However, while head length appears a poor indicator of hatchling total size, it is a reasonably precise indicator of incubation environment. For example, Ferguson (1985) catalogued environmentally induced developmental abnormalities in crocodilians, and found head defects to be among the most commonly occurring. Also, Webb, Beal, Manolis and Dempsey (1987) found head development to be very closely linked to incubation environment in *C. johnstoni*. Therefore, rather than head length being a reflection of size, it is most probably a reflection of the optimality of the incubation environment.

The slender evidence for directional selection in head length may simply result from the fact that among those animals released, the distribution of head length was not perfectly normal.
distribution of head length displays no statistically significant evidence of non-normality, the distribution of head length among those animals recaptured is even more normal. Therefore the apparent shift in mean head length may simply be a reflection of the increased normality of the distribution of head length.

6.4.3 HATCHLING SURVIVAL

Hatchling survival is not random, and most correlates of survival relate to the incubation environment. As has been amply demonstrated, there is some association between head length and survival, though the biological basis of that relationship remains obscure.

Temperature at three points during incubation has been identified as a correlate of hatchling survival. However, whether those periods are related to survival depends apparently on the thermal environments of the particular year in question.

The three particular points are in themselves interesting. The onset of post-laying embryonic development during the 0-10% period could, a priori, be expected to be critical, as it would initiate a developmental trajectory which may not be fully correctable later in incubation. The second sensitive period, between 60-70% of incubation, coincides approximately with the end of organogenesis, which is another period which one would expect to be critical (Ferguson 1985; Webb, Beal, Manolis and Dempsey 1987). The final period of temperature sensitivity, 80-90% of incubation, is not directly attributable to any
particular embryonic event. It is after the completion of organogenesis, but before the onset of residual yolk internalisation (Webb, Beal, Manolis and Dempsey 1987). However, that period does approximately coincide with the peak of metabolic heat production (Whitehead 1987a, b). It may thus be possible that there needs to be some matching of the external environment and metabolic heat production during that critical period. If temperatures were too high then the metabolic heat production might raise nest temperature too high. Conversely, if environmental temperatures were too low, then too much of the embryonic heat production might be lost to the environment.

Lang (1985) suggests that the temperature of egg incubation may influence thermal selection be hatchlings of Crocodylus siamensis: as hatchlings, embryos incubated at higher temperatures selected higher temperatures. If the assertion of Lang (1985) is correct, then behavioural differences may exist among hatchlings due to differences in incubation environment.

Miller et al. (1985) found that locomotor performance of hatchling snapping turtles, Chelydra serpentina, was influenced by the hydric environment experienced by the embryo. The pattern observed was that embryos which had been exposed to hydric stress were more slow moving both on land and in water.

The results of Lang (1985) and Miller et al. (1985) strongly suggest that the incubation environment experienced by an embryo may play a large role in determining the behavioural phenotype of the resulting hatchling. The action of natural selection on the
behavioural phenotype of the lizard *Uta stansburiana* has been amply demonstrated by Fox (1978).

One qualification that must be made on the foregoing argument concerns the design of the experiment. By transferring hatchlings from their natal pool, any parental care that might have occurred would have been circumvented. The formation of creches with an adult crocodile in attendance has been noted in *C. johnstoni* (Webb, Buckworth and Manolis 1983d). It has been assumed that the presence of an adult crocodile may deter predators of the hatchlings, though this has not been demonstrated. No individuals of *C. johnstoni* have ever attacked people collecting hatchlings, though a threat display by an adult has been observed at least once (Webb et al. unpublished observation).

The hatchlings released into Site One were found to form loose aggregations similar to creches, though they were obviously made up of more that one clutch. Multiple clutch creches have been observed in *C. johnstoni* (this study; Webb et al. unpublished observation). Such clutches appear to have only a single larger *C. johnstoni* in attendance and whether or not that crocodile was a parent of any of the hatchlings in the creches has not been established.

The possible influence of the lack of parental care that characterised this experiment is unknown. Given that cannibalism was identified as a cause of mortality, it is possible that at least this source of loss would have been prevented by parental care. That hatchlings under truly natural circumstances have been reported to
exhibit scarring consistent with attack by turtles (Webb, Buckworth and Manolis 1983d) suggests that parental care may not be effective at least against this predator. In general, while parental care was lacking in this experiment, it is considered unlikely that this biased the results to any great extent.
Table 6.1 Dimensions of hatchlings released in 1984 and 1985, with a comparison of variances and means.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>1984</th>
<th>1985</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N=246)</td>
<td>(N=139)</td>
<td></td>
</tr>
<tr>
<td>Head length (cm)</td>
<td>3.73 0.009</td>
<td>3.73 0.012</td>
</tr>
<tr>
<td>Snout-vent length (cm)</td>
<td>11.64 0.168</td>
<td>11.44 0.123</td>
</tr>
<tr>
<td>Trunk length (cm)</td>
<td>7.91 0.116</td>
<td>7.71 0.074</td>
</tr>
<tr>
<td>Total weight (g)</td>
<td>45.55 20.162</td>
<td>42.00 18.877</td>
</tr>
<tr>
<td>Residual yolk weight (g)</td>
<td>7.89 4.846</td>
<td>6.36 3.774</td>
</tr>
<tr>
<td>Yolk-free weight (g)</td>
<td>37.67 13.450</td>
<td>35.64 9.423</td>
</tr>
<tr>
<td>Days exposure</td>
<td>19.94 47.576</td>
<td>18.84 42.207</td>
</tr>
</tbody>
</table>

* 0.05 > P > 0.01, ** 0.01 > P > 0.001, *** 0.001 > P
Table 6.2 Dimensions of hatchlings recaptured in 1984 and 1985, with a comparison of variances and means.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>1984 (N=110)</th>
<th>1985 (N=65)</th>
<th>F</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head length (cm)</td>
<td>3.75 0.007</td>
<td>3.74 0.008</td>
<td>1.14</td>
<td>0.74</td>
</tr>
<tr>
<td>Snout-vent length (cm)</td>
<td>11.69 0.115</td>
<td>11.43 0.121</td>
<td>1.05</td>
<td>4.67***</td>
</tr>
<tr>
<td>Trunk length (cm)</td>
<td>7.94 0.088</td>
<td>7.70 0.081</td>
<td>1.08</td>
<td>5.25***</td>
</tr>
<tr>
<td>Total weight (g)</td>
<td>45.39 15.834</td>
<td>42.40 20.960</td>
<td>1.32</td>
<td>4.54***</td>
</tr>
<tr>
<td>Residual yolk weight (g)</td>
<td>7.79 4.335</td>
<td>6.41 3.267</td>
<td>1.33</td>
<td>4.44***</td>
</tr>
<tr>
<td>Yolk-free weight (g)</td>
<td>37.60 10.396</td>
<td>35.99 10.018</td>
<td>1.04</td>
<td>3.21**</td>
</tr>
<tr>
<td>Days exposure</td>
<td>21.58 37.805</td>
<td>14.66 29.633</td>
<td>1.28</td>
<td>7.50***</td>
</tr>
</tbody>
</table>

* 0.05 > P > 0.01, ** 0.01 > P > 0.001, *** 0.001 > P
Table 6.3 Comparison of means and variances of six parameters among survivors and non-survivors in 1984

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>SURVIVORS (N=110)</th>
<th>NON-SURVIVORS (N=136)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MEAN</td>
<td>VARIANCE</td>
</tr>
<tr>
<td>Head length (cm)</td>
<td>3.75</td>
<td>0.005</td>
</tr>
<tr>
<td>Snout-vent length (cm)</td>
<td>11.69</td>
<td>0.115</td>
</tr>
<tr>
<td>Trunk length (cm)</td>
<td>7.94</td>
<td>0.088</td>
</tr>
<tr>
<td>Total weight (g)</td>
<td>45.39</td>
<td>15.834</td>
</tr>
<tr>
<td>Residual yolk weight (g)</td>
<td>7.79</td>
<td>4.335</td>
</tr>
<tr>
<td>Yolk-free weight (g)</td>
<td>37.60</td>
<td>10.396</td>
</tr>
</tbody>
</table>

* 0.05 > P > 0.01,  ** 0.01 > P > 0.001,  *** 0.001 > P
Table 6.4 Comparison of means and variances of six parameters among survivors and non-survivors in 1985

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>MEAN</th>
<th>VARIANCE</th>
<th>MEAN</th>
<th>VARIANCE</th>
<th>F</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head length (cm)</td>
<td>3.74</td>
<td>0.008</td>
<td>3.71</td>
<td>0.015</td>
<td>1.87**</td>
<td>1.65</td>
</tr>
<tr>
<td>Snout-vent length (cm)</td>
<td>11.43</td>
<td>0.121</td>
<td>11.44</td>
<td>0.126</td>
<td>1.04</td>
<td>0.17</td>
</tr>
<tr>
<td>Trunk length (cm)</td>
<td>7.70</td>
<td>0.081</td>
<td>7.73</td>
<td>0.067</td>
<td>1.21</td>
<td>0.65</td>
</tr>
<tr>
<td>Total weight (g)</td>
<td>42.40</td>
<td>20.960</td>
<td>41.65</td>
<td>17.041</td>
<td>1.23</td>
<td>1.02</td>
</tr>
<tr>
<td>Residual yolk weight (g)</td>
<td>6.41</td>
<td>3.267</td>
<td>6.31</td>
<td>4.266</td>
<td>1.31</td>
<td>0.30</td>
</tr>
<tr>
<td>Yolk-free weight (g)</td>
<td>35.99</td>
<td>10.018</td>
<td>35.34</td>
<td>8.833</td>
<td>1.13</td>
<td>1.24</td>
</tr>
</tbody>
</table>

* 0.05 > P > 0.01, ** 0.01 > P > 0.001, *** 0.001 > P
Table 6.5. The predicted relationship between mean nest temperature during 80-90% of incubation and the probability of hatchling survival in 1984.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Survival</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>31.3</td>
<td>0.3381</td>
<td>0.0667</td>
</tr>
<tr>
<td>33.6</td>
<td>0.6947</td>
<td>0.0773</td>
</tr>
<tr>
<td>34.4</td>
<td>0.4575</td>
<td>0.0649</td>
</tr>
</tbody>
</table>
Table 6.6. The predicted relationship between mean nest temperature during 0-10% of incubation and the probability of hatchling survival in 1985.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Survival</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>27.0</td>
<td>0.8959</td>
<td>0.0361</td>
</tr>
<tr>
<td>28.5</td>
<td>0.4700</td>
<td>0.0928</td>
</tr>
<tr>
<td>30.0</td>
<td>0.1933</td>
<td>0.0472</td>
</tr>
</tbody>
</table>
Table 6.7. The predicted relationship between mean nest temperature during 60-70% of incubation and the probability of hatchling survival in 1985.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Survival</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>30.2</td>
<td>0.2981</td>
<td>0.0558</td>
</tr>
<tr>
<td>32.0</td>
<td>0.4665</td>
<td>0.0433</td>
</tr>
<tr>
<td>33.4</td>
<td>0.7655</td>
<td>0.0520</td>
</tr>
</tbody>
</table>
Table 6.8. The characteristics of the nest temperatures found to be significantly related to hatchling survival in 1984 and 1985.

<table>
<thead>
<tr>
<th>Year</th>
<th>Period</th>
<th>Minimum</th>
<th>Mean</th>
<th>Maximum</th>
<th>Variance</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>0-10%</td>
<td>25.69</td>
<td>27.58</td>
<td>30.27</td>
<td>1.74</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>60-70%</td>
<td>28.31</td>
<td>31.13</td>
<td>33.10</td>
<td>2.98</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>80-90%</td>
<td>29.73</td>
<td>32.84</td>
<td>34.97</td>
<td>3.47</td>
<td>17</td>
</tr>
<tr>
<td>1985</td>
<td>0-10%</td>
<td>26.98</td>
<td>29.00</td>
<td>30.79</td>
<td>1.76</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>60-70%</td>
<td>30.84</td>
<td>32.49</td>
<td>33.86</td>
<td>0.87</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>80-90%</td>
<td>32.64</td>
<td>33.90</td>
<td>35.05</td>
<td>0.55</td>
<td>13</td>
</tr>
</tbody>
</table>
Table 6.9. Change in hatchling dimensions during the survival experiment in 1984 and 1985 with a comparison of means and variances.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>1984</th>
<th>1985</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N=110)</td>
<td>(N=65)</td>
<td></td>
</tr>
<tr>
<td>Head length (cm)</td>
<td>MEAN 0.61</td>
<td>MEAN 0.48</td>
</tr>
<tr>
<td></td>
<td>VARIANCE 0.012</td>
<td>VARIANCE 0.017</td>
</tr>
<tr>
<td>Snout-vent length (cm)</td>
<td>MEAN 1.39</td>
<td>MEAN 1.07</td>
</tr>
<tr>
<td></td>
<td>VARIANCE 0.108</td>
<td>VARIANCE 0.104</td>
</tr>
<tr>
<td>Trunk length (cm)</td>
<td>MEAN 0.78</td>
<td>MEAN 0.59</td>
</tr>
<tr>
<td></td>
<td>VARIANCE 0.074</td>
<td>VARIANCE 0.055</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>MEAN -5.93</td>
<td>MEAN -3.81</td>
</tr>
<tr>
<td></td>
<td>VARIANCE 2.953</td>
<td>VARIANCE 4.465</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F 1.42</td>
<td>F 1.04</td>
</tr>
<tr>
<td></td>
<td>t 7.06**</td>
<td>t 6.27**</td>
</tr>
<tr>
<td></td>
<td>F 1.34</td>
<td>t 4.69**</td>
</tr>
<tr>
<td></td>
<td>t 7.23**</td>
<td></td>
</tr>
</tbody>
</table>

* 0.05 > P > 0.01,  ** 0.01 > P > 0.001,  *** 0.001 > P
Fig. 6.1. The distribution of head length at hatching of surviving and non-surviving *C. johnstoni* hatchlings in 1984.
Survivors

Non-survivors

Number of individuals

Head length (cm)

3.5 3.6 3.7 3.8 3.9 4.0 4.1 4.2
Fig. 6.2. The distribution of head length at hatching of surviving and non-surviving *C. johnstoni* hatchlings in 1985.
Fig. 6.3. The distribution of *C. johnstoni* hatchling survival and non-survival with respect to days exposure in 1984.
Fig. 6.4. The distribution of *C. johnstoni* hatchling survival and non-survival with respect to days exposure in 1985.
Fig. 6.5. The relationship between the cumulative number of hatchlings released and the cumulative number known to have survived.
Fig. 6.6. The predicted relationship between the probability of hatchling survival and head length for hatchlings released in 1984.
Fig. 6.7. The predicted relationship between the probability of hatchling survival and head length for hatchlings released in 1985.
Probability of survival

Head length (cm)
SYNTHESIS AND CONCLUSIONS

7.1 GENERAL

This study complements the numerous studies of Webb and coworkers in providing a body of ecological data which is the most extensive for a single population of any long lived reptile. It also presents our first reasonably comprehensive study of the ecology of environmental sex determination at the level of both the population and the individual.

In the introductory Chapter of this thesis, five specific questions were posed in defining the central theme of this thesis, namely whether there is a relationship between population structure/dynamics and the operation of ESD. Each of these questions will now be addressed in the light of what has been established in, or can be suggested from, the data and the analyses contained in the foregoing Chapters.

7.2 ANSWERS TO FIVE QUESTIONS

1. Do females select nests sites with reference to environmental cues, and if so, which cues?

Nest site selection by a crocodile in response to environmental cues was identified here for the first time. Even though
the results reported are from a limited study, it is clear that crocodiles tend to avoid grassed areas and select nest sites with temperatures of at least $28^\circ C$ some 20cm below the surface at 18.00 hours. The data analysis suggested that females conduct trial excavations on the basis of the temperature at the surface of the soil, although this may not be an accurate guide to subsurface temperature. The delay between first digging and laying may well reflect the time required for subsurface temperatures to increase to an acceptable level.

2 Within a nesting season, is there an ordering of females with respect to time of nesting, and if so, is there an association between time of nesting and the sex ratio of the resulting embryos?

Large females tend to nest before small females. On the basis of relationship between estimated size and day of nesting, it would appear that the observed relationship between size and day of nesting is in reality a relationship between age and day of nesting, with old females laying before young females. It is the day on which a clutch is laid that is the primary determinant of the thermal environment the embryos will experience during their development. The thermal environment is the primary determinant of embryonic sex. There is a relationship between day of laying and sex ratio such that early and late laid clutches tend to produce females, whereas clutches laid in the middle of the nesting season tend to produce males. This implies that old and young females tend to produce female offspring whereas middle aged females produce males.
3 What environmental correlates of hatchling sex ratio exist, and when and in what fashion do they operate?

Sex is determined during that period between 20 and 50% of incubation. In particular, it is the mean temperature between 20 and 30% of incubation that plays the major role in the production of males. However, the affect of the temperature experienced during that period is moderated by changes in mean temperature during the next 20% of incubation. An influence of substrate type was also confirmed and is interpreted to reflect variation in the hydric environment of the embryos. Females are produced at high and low temperatures and males at intermediate temperatures.

4 What environmental correlates of embryonic survival exist, and are they the same as those correlates of hatchling sex ratio?

The most important cause of embryo mortality, predation by goannas, was found to be effectively random among those nests taken soon after laying. Flooding was not found to show a significant influence in this study. Other than these factors, embryo survivorship was found to be generally high. Influences of substrate type, egg depth and the exposure to low temperatures late in incubation were noted, but the magnitude of those effects suggests they play at best only a very minor role. Thus, there appears to be no important association between those variables which affect sex determination and those which influence embryo survival.
5 Is hatchling survival random, and if not, what phenotypic correlates of survival exist, and does hatchling survival relate in some way to the incubation environment?

Hatchling survival is clearly not random. Nor is it related to hatchling size per se. The affect of stabilising selection was apparent, though its pattern may have been different in the two years where it was examined. Head length was the most important correlate of hatchling survival, and it is suggested that head length acts as a measure of the optimality of the incubation environment. Particularly low temperatures early in incubation, and particularly high temperatures at the end of organogenesis, are correlated with a higher probability of hatchling survival. Extreme temperatures during the period of maximal metabolic heat production toward the end of incubation were associated with a lower probability of hatchling survival. Hatchling survival does not, however, appear to be related to the sex of the hatchling.

7.3 IS THERE A GENERAL PATTERN TO SEX DETERMINATION AND SURVIVAL IN CROCODILES?

Male *C. johnstoni* apparently tend to be the offspring of middle aged females, which nest in the middle of the nesting season. The thermal environment which an embryo experiences during incubation is largely determined by the day on which the egg is laid. Early laid nests tend to be cooler than later laid nests. Moreover, the initial and final temperatures of clutches are positively correlated. Thus, early laid nests tend to be consistently cooler than late laid nests at a given stage of incubation.
Hatchling survival reflects the action of stabilising selection, yet a survival advantage is sometimes conferred both by low temperatures early in incubation and high temperatures later in incubation, as was observed in 1985. Thus, it appears that there may sometimes be a survival advantage in coming from an early or a late laid nest. The data for 1984 suggest that, in the final stages of incubation, intermediate temperatures are optimal for subsequent survival. The non-significant sex ratio shifts in hatchling survival agree with these conclusions. In 1984, males survived more commonly than did females, and in 1985, females survived more commonly than did males.

Although the data presented in this thesis reflect a considerable variation between years, it would appear that, on average, males are produced from optimal incubation environments and that this represents a survival advantage to the hatchling. Thus, natural selection would appear to have acted in such a way that a middle aged female in the prime of her reproductive life should tend to produce male offspring which experience an optimal incubation environment and which, in turn, confers a maximal probability of survival as a hatchling. Whether that incubation environment confers maximal post-hatching growth was not investigated although, from other studies, this appears likely.
7.4 ON THE EVOLUTION AND MAINTENANCE OF ENVIRONMENTAL SEX DETERMINATION

"Fitness enters population biology as a vague heuristic notion, rich in metaphor but poor in precision."

(R. Levins)

In retrospect, there are reasons for believing that the design of this study may have been inappropriate for addressing the broader issues of the evolution of ESD. Nevertheless, the findings of this study throw some light on the evolution and maintenance of ESD. For example, it is clear that the operation of ESD in *C. johnstoni* is intimately related to the structure and dynamics of the population. Whether that relationship was involved in the evolution of ESD, as it seems to be in the maintenance of ESD, is unknown. However, to postulate the operation of different factors in the evolution and the maintenance of ESD is certainly not parsimonious. How well, then, do the hypotheses of Charnov and Bull (1977) and of Webb and Smith (1984), as currently interpreted, agree with the results of this study?

Charnov and Bull's thesis requires that the egg incubation environment affects the fitness of the sexes differentially, and that selection acts to allow the matching of the appropriate sex to the appropriate environment. In these terms, the evolution of ESD appears to have been driven by sexual selection. As a result, any interaction between the action of ESD and population structure would be fortuitous.
Webb and Smith suggested that ESD arose through the survival advantages inherent in coupling the timing of sexual differentiation to the environment. They also suggest that the allocation of the sexes to particular environments occurred subsequent to the evolution of ESD and was driven by different selective forces. Thus, the observed interaction between ESD and population structure would be the result of selection.

The data presented in this thesis neither confirm nor deny either hypothesis although, on balance, that of Webb and Smith may be more parsimonious. Additionally, the relationship between the age of a female and the sex of her offspring suggests the operation of selective forces of a kind not previously considered. While such forces can readily be accommodated in the model of Webb and Smith, it is unclear whether this applies to the model of Charnov and Bull.

7.5 INDICATIONS FOR FURTHER WORK

There are three principal directions in which future research on the population dynamics and ecology of *C. johnstoni* might be directed: first, to determine the precise basis of the ordering of females during the nesting season; second, to examine whether females of different ages or sizes select different types of nest site; and third, to consider whether any form of altruism operates in this species.

Of more general interest is the need to examine the determinants of hatchling head length. If, as suggested here, head
length reflects the optimality of the incubation environment then it follows that, because of the number of variables operating in the field, much of the variance in head length cannot accounted for even though egg weight is its strongest correlate. An extension of this is to determine precisely how the optimality of the incubation influences survival. That the incubation environment may influence the behaviour and locomotor performance of hatchlings would appear to be an obvious place to begin such an investigation.

With reference to the evolution and maintenance of ESD, it is unlikely that detailed ecological studies will be particularly informative. As identified above, the major difference between the hypotheses of Charnov and Bull and of Webb and Smith is that the former requires sexual selection and the latter requires selection for embryo survival. Given that many reptile species have been now examined for the existence of ESD, a growing body of data is becoming available which will allow comparative studies of the nature and extent of sexual selection in species with and without ESD to be undertaken. What are lacking, however, are comparable data on the constraints on embryo survival in species with and without ESD.
LITERATURE CITED


dependent sex determination in two suborders of turtles.
*Copeia* 1985: 784-786.


ratio in turtles with environmental sex determination.
*Evolution* 36: 333-341.

temperatures in turtles: a geographic comparison. *Evolution*
36: 326-332.


Bulmer, M.G. and Bull, J.J. 1982. Models of polygenic sex

Bulnheim, H-P. 1978. Interaction between genetic, external and
parasitic factors in sex determination of the crustacean
amphipod *Gammarus duebeni*. *Helgolander wiss. Meeresunters* 3:
1-33.

Burbidge, A.A. 1987. The management of crocodiles in Western
Australia. In *Wildlife Management: Crocodiles and Alligators*,
127. Surrey Beatty and Sons: Sydney.

Carr, J.L. and Bickham, J.W. 1981. Sex chromosomes of the Asian black
pond turtle, *Siebenrockiella crassicollis* (Testudines: *Emydidae*).


Cott, H.B. 1957. *Interim report on the ecology of Crocodylus niloticus in Northern Rhodesia*. Unpublished mimeograph report to the Director of Game and Tsetse Control.


Graham, A. 1968. The Lake Rudolf crocodile (Crocodylus niloticus Laurenti) population. Mimeograph Report from Wildlife Services Ltd. to the Kenya Game Department.


Webb, G., Manolis, S., Whitehead, P. and Letts, G. 1984. A proposal for the transfer of the Australian population of *Crocodylus porosus* Schneider (1801), from Appendix I to Appendix II of


APPENDIX 1

PIVOTAL, THRESHOLD AND SEX DETERMINING TEMPERATURES:
VARIATION IN CARETTA CARETTA AND GRAPTEMYS PSEUDOGEOGRAPHICA

Submitted to Copeia May 1987
Environmental Sex Determination (ESD) in reptiles has attracted considerable interest in recent years. Most studies are laboratory-based and use temperature as the variable environmental parameter. This has lead to the unfortunate and perhaps misleading (Webb and Smith 1984; Webb et al. 1987; Hutton 1987) terminology of Temperature-dependent Sex Determination (TSD; Bull 1980). In the discussion of the relationship between temperature and sex, most interest centres on that range of temperatures over which sex ratio changes from one extreme to the other, i.e. from all male to all female or vice versa. Under the models proposed and developed by Charnov and Bull (1977), Bull et al. (1982a, b), Bull (1983), and Bulmer and Bull (1982), both the rate of change of sex ratio (expressed as the proportion of males in the sample) with respect to temperature over this range and the point at which a 0.50 sex ratio is produced is expected to be under the influence of natural selection. The existing data for reptiles are, however, equivocal in relation to this point.

The terms pivotal temperature (Mrosovsky and Yntema 1980) and threshold temperature (Bull 1980) were used to describe the approximate temperature at which the sex ratio changes most rapidly. Both terms were subsequently defined as that temperature which produces a 0.50 sex ratio (Bull et al. 1982b; Mrosovsky 1984). Limpus et al. (1983, 1985) defined Sex Determining Temperature 50 (SDT 50) in the same fashion, but this parameter differs in that it is a theoretical temperature which is estimated statistically, rather than being inferred as in the case of the pivotal or threshold temperature. The method used by Limpus et al. (1983, 1985) followed that of
Litchfield and Wilcoxon (1949) and is both crude and approximate. It is an inexact method compared to probit analysis for dealing with such data (Finney 1971, 1978; Hubert 1980). It is proposed here to adopt a standard terminology for the range of temperatures over which sex ratio changes, as well as for that temperature which produces a 0.50 sex ratio. Furthermore, probit analysis is recommended for this purpose. Probit analysis has already been used in an analysis of the relationship between total incubation time and sex ratio in the sea turtles *Chelonia mydas* and *Dermochelys coriacea* (Mrosovsky et al. 1984).

The range of temperatures over which sex ratio changes may be defined as the Transition Zone (TZ). The TZ is characterised by two temperatures (expressed in °C), one of which produces 95% male (see below) and the other produces 95% female. The higher of the two is denoted the TZ$_U$ and the lower the TZ$_L$. The breadth of the TZ, i.e. the difference between the TZ$_U$ and the TZ$_L$, is defined as the transition interval (TI; expressed in °C). The temperature which produces a 0.50 sex ratio is well described by the pivotal temperature (expressed in °C), and its use is recommended. For example, the Tennessee population of *Graptemys pseudogeographica* has a TZ$_U$ of 29.74°C, a TZ$_L$ of 28.26°C, and hence a TI of 1.48°C (Table 3). It also has a pivotal temperature for 29.00°C (Table 3).

The use of TZ's and pivotal temperatures requires that only males are produced at one temperature and only females at another temperature. Some species, such as *Crocodylus johnstoni* which does not produce all males at any constant temperature (Webb and Smith 1984;
Webb et al. (1987), is clearly not amenable to analyses involving TZ and pivotal temperature estimation. The limits of the TZ are best estimated from within the TZ, and any statistical estimate of the pivotal temperature by probit analysis requires at least two data points within the TZ, while more than one data point on either side of the TZ is superfluous. In these terms, the majority of published data sets are of no use for estimating TZ's and pivotal temperatures.

We will consider data for six clutches of Caretta caretta (Limpus et al. 1985), and approximately 35 of Graptemys pseudogeographica (Bull et al. 1982b). The six C. caretta clutches have been regarded as demonstrating marked variation in the pivotal temperature, both within and between populations (Limpus et al. 1985). The 35 G. pseudogeographica clutches include samples from two different populations (25 from Wisconsin, 10+ from Tennessee) which have also been suggested to demonstrate interpopulation variation pivotal temperature (Bull et al. 1982b).

The eight data sets were analysed by regression modelling using a probit link function and binomial error distribution (Genstat). The six C. caretta clutches were subjected to pairwise comparisons to determine if any of them displayed significant parallelism (i.e. the relationship between sex ratio and temperature showed a significant shift sideways) or non-colinearity (i.e. a significant change in the rate of change in sex ratio with respect to temperature).
The initial results of this analysis (Table 1) identified three possible groups among the *C. caretta* clutches on the basis of parallelism. Clutches CC2 and CC3 differ from clutches CC1, CC4 and CC5, and there are no significant differences within these two groups. The clutches in these two groups were thus pooled to form two data sets. Since the remaining clutch, CC6, differs from neither group, it was treated as an individual clutch. The pairwise regression modelling was then repeated on the three (CC2,3, CC1,4,5 and CC6) data sets.

The re-analysis indicated (Table 2) that CC2,3 and CC1,4,5 exhibited significant parallelism, but no evidence of non-colinearity. The remaining clutch (CC6) was not different to either, but was marginally more similar to CC2,3 ($\chi^2_1 = 1.3930$ versus 1.747). Given that CC6 was not significantly different from either CC2,3 or CC1,4,5, it was retained as a separate entity. Probit analysis (SAS) using the three data sets was then used to derive pivotal temperatures (Table 3).

The data for *G. pseudogeographica* were treated in the same manner as the *C. caretta* data. The two data sets exhibited parallelism ($\chi^2_1 = 24.989; P < 0.05$), but no significant non-colinearity was demonstrated ($\chi^2_1 = 0.040; P > 0.05$). The pivotal temperatures are given in Table 3.

The nature of probit analysis is such that values of zero and one are impossible. Thus, a probit model will predict an infinite TZ, as there is always a finite, though vanishingly small, probability of occurrence of that sex which is not observed at a particular
temperature. Therefore, some decision must be made as to which probability can be taken to define the boundary of the TZ. Given the nature of the problem, it is reasonable to adopt a $P = 0.05$ limit to the TZ, i.e. the limits of the TZ are those temperatures which are predicted to produce 5% of one sex. The upper limit of the TZ should be denoted the $T_{ZU}$ and the lower limit the $T_{ZL}$. The TZ’s of the *C. caretta* and *G. pseudogeographica* as predicted by probit analysis are given in Table 3.

Bull et al. (1982b) suggested that the pivotal temperatures of the Wisconsin and Tennessee populations of *G. pseudogeographica* differed by no more than $0.50^\circ C$. The probit analyses performed here demonstrate that the pivotal temperatures differ by $0.43^\circ C$ and that this difference is significant. However, the contentions of Limpus et al. (1985), concerning variation in pivotal temperature in *C. caretta* are not fully supported. Clutches CC1,2,3 represent a sample from one site and CC4,5,6 a sample from a separate site. The analyses presented here indicate that it would be inappropriate to pool the clutches on the basis of sites, as it would mask real variation which does not assort with respect to these sites (Tables 1-3). However, there is real variation in pivotal temperature and there appear to be at least two values represented in the six clutches examined. The pivotal temperature inferred for *C. caretta* from North America ($30^\circ C$; Yntema and Mrosovsky 1980, 1982) is higher than both of those reported here, but the data available for North America are inadequate for probit analysis, so it is not yet possible to determine whether this difference is significant.
Perhaps more important than the quantification of variation in pivotal temperature is the manner in which that variation arises. Where variation in pivotal temperature exists, it occurs through a shift in TZ. Thus, the rate of change in sex ratio with respect to temperature appears invariant within a species, but the range of temperature over which that change occurs varies (i.e. the TI is constant). Additionally, the TI's of *C. caretta* and *G. pseudogeographica* are markedly different (Table 3), and this difference is perhaps correlated with environmental variance being greater among nests of *G. pseudogeographica* than among nests of *C. caretta*. 


Table 1. Probit analysis of the relationship between sex ratio and temperature for six Caretta caretta clutches (data from Limpus et al. 1985). The $\chi^2$ of parallelism appears above the diagonal, and the $\chi^2$ of non-collinearity appears below the diagonal. * significant at the 0.05 level.

<table>
<thead>
<tr>
<th>Clutch</th>
<th>CC1</th>
<th>CC2</th>
<th>CC3</th>
<th>CC4</th>
<th>CC5</th>
<th>CC6</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC1</td>
<td>7.4290*</td>
<td>3.9962*</td>
<td>0.0800</td>
<td>0.1040</td>
<td>1.5500</td>
<td></td>
</tr>
<tr>
<td>CC2</td>
<td>0.5900</td>
<td>2.5454</td>
<td>9.4565*</td>
<td>10.2296*</td>
<td>1.8281</td>
<td></td>
</tr>
<tr>
<td>CC3</td>
<td>5.0786*</td>
<td>2.6175</td>
<td>4.5565*</td>
<td>8.8935*</td>
<td>0.5779</td>
<td></td>
</tr>
<tr>
<td>CC4</td>
<td>3.3620</td>
<td>1.3287</td>
<td>0.2151</td>
<td>1.1544</td>
<td>0.4890</td>
<td></td>
</tr>
<tr>
<td>CC5</td>
<td>0.9980</td>
<td>0.1051</td>
<td>1.4588</td>
<td>0.5725</td>
<td>2.3426</td>
<td></td>
</tr>
<tr>
<td>CC6</td>
<td>0.4560</td>
<td>0.0100</td>
<td>2.9568</td>
<td>1.5840</td>
<td>0.1753</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Probit analysis of the relationship between sex ratio and temperature for six Caretta caretta clutches pooled on the basis of the previous analysis (Table 1). The $\chi^2_1$ of parallelism appears above the diagonal, and the $\chi^2_1$ of non-collinearity appears below the diagonal. * significant at the 0.05 level.

<table>
<thead>
<tr>
<th>Data set</th>
<th>CC2,3</th>
<th>CC1,4,5</th>
<th>CC6</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC2,3</td>
<td>-</td>
<td>16.8490*</td>
<td>1.3930</td>
</tr>
<tr>
<td>CC1,4,5</td>
<td>0.2670</td>
<td>-</td>
<td>1.7470</td>
</tr>
<tr>
<td>CC6</td>
<td>0.4300</td>
<td>0.0660</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3. Pivotal temperatures, TZ’s and TI’s predicted for three *Caretta caretta* and two *Graptemys pseudogeographica* data sets. The upper and lower 95% confidence limits of the pivotal temperatures (PT’s) are represented by the PT\textsubscript{U} and PT\textsubscript{L} respectively.

<table>
<thead>
<tr>
<th>Data Set</th>
<th>PT\textsubscript{L}</th>
<th>PT</th>
<th>PT\textsubscript{U}</th>
<th>TI</th>
<th>TZ\textsubscript{L}</th>
<th>TZ\textsubscript{U}</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. caretta</em> 2,3</td>
<td>26.98</td>
<td>27.49</td>
<td>27.97</td>
<td>4.51</td>
<td>25.23</td>
<td>29.74</td>
</tr>
<tr>
<td><em>C. caretta</em> 1,4,5</td>
<td>28.47</td>
<td>28.92</td>
<td>29.41</td>
<td>5.17</td>
<td>26.34</td>
<td>31.51</td>
</tr>
<tr>
<td><em>C. caretta</em> 6</td>
<td>26.31</td>
<td>28.10</td>
<td>29.23</td>
<td>5.61</td>
<td>25.30</td>
<td>30.91</td>
</tr>
<tr>
<td><em>G. pseudogeographica</em> (Tennessee)</td>
<td>28.83</td>
<td>29.00</td>
<td>29.13</td>
<td>1.48</td>
<td>28.26</td>
<td>29.74</td>
</tr>
<tr>
<td><em>G. pseudogeographica</em> (Wisconsin)</td>
<td>29.32</td>
<td>29.43</td>
<td>29.52</td>
<td>1.42</td>
<td>28.72</td>
<td>30.14</td>
</tr>
</tbody>
</table>
APPENDIX 2

A METHOD FOR ESTIMATING RESIDUAL YOLK MASS
IN HATCHLING CROCODILIANS
logica 29:327-342


WADE C. SHERBROOKE
Department of Ecology and Evolutionary Biology
University of Arizona
Tucson, Arizona 85721, USA

Present address.
Southwestern Research Station
The American Museum of Natural History
Portal, Arizona 85632, USA

**TECHNIQUES**

**A METHOD FOR ESTIMATING RESIDUAL YOLK MASS IN HATCHLING CROCODILES**

During the later stages of embryonic development, birds and reptiles typically internalize the vitelline sac, which contains a supply of yolk (Romaniol 1960; Ewert 1979; Ferguson 1985). The residual yolk (Romaniol 1960) thus formed represents a significant source of nutrition for the immediate post-hatching period. The selective advantages of residual yolk masses have been speculated upon by a number of authors (for example Ferguson and Joanne 1982, 1983, and Packard et al. 1981). To measure the amount of residual yolk accurately, hatchlings need to be sampled but this precludes their use in further experiments. Furthermore, sacrificing large numbers of crocodilian hatchlings cannot sometimes be justified on conservation grounds (Gans and Pooley 1976). We derived a simple method for predicting residual yolk mass from abdomen dimensions in Crocodylus johnstoni, which has allowed us to use residual yolk mass as a variable in experiments which examine the relationship between incubation environment and post-hatching growth and survivorship. The method should be applicable to other crocodilians and perhaps lacertilians.

Thirty-seven C. johnstoni hatchlings from eggs incubated at different temperatures were sacrificed on the day they hatched. Prior to administering a lethal overdose of Nembutal (Sodium pentobarbital), each hatchling was laid on its back and had the maximum width of the abdomen from right to left (A in centimeters) and the maximum width of the umbilical scar (U in centimeters) measured with calipers. Total hatching mass (residual yolk mass plus hatching mass), head length, snout-vent length and total length of each individual were also measured (Table 1). After death, the residual yolk was removed and weighed (Table 1).

Least squares multiple regression analysis (GENSTAT) was used to predict residual yolk mass (in grams) from combinations of the measurements taken. Both A and U accounted for significant amounts of the total variance in residual yolk mass (83%, $F_{1,33} = 353.57, P < 0.001;$ and 7% $F_{1,33} = 32.23, P < 0.001$ respectively). Additionally, various transformations of the parameters measured were computed (square root, square, natural logarithm) and then tested in the regression in an attempt to improve the overall fit. The square transformation used was computed as the square of the individual's deviation from the sample mean for a particular parameter. This allows a statistically sound method to model a parabolic relationship. Of those tested, only the square of the deviation of each individual hatchling's mass from the mean mass of the sample 47.2 g (WSTD) accounted for a significant amount of the total variance (2%, $F_{1,33} = 8.38, 0.01 > P > 0.001$).

The model which explained most variation ($92%$) in residual yolk mass was:

$$\text{VAR(YOLK)} = -1.055 + 0.842A - 0.459U - 0.0019\text{WSTD}$$

The natural logarithmic transformation generates an asymmetrical error equivalent to approximately ± 1 g. For an independent sample of animals ($n = 8$), which died on the day of hatching or were sacrificed as part of another experiment, prediction errors ranged from 0.0 g (3%) to 1.8 g (19%), and averaged $-0.1 \pm 1.1$ g (SD).

**LITERATURE CITED**


ANTHONY M.A. SMITH and

GRAHAME J.W. WEBB

1. Research School of Biological Sciences
2. University of New South Wales
3. School of Zoology
4. Australian National University

1. Kensington, N.S.W. 2033 AUSTRALIA
2. University of New South Wales
3. Kensington, N.S.W. 2033 AUSTRALIA
4. Canberra, A.C.T. 2601 AUSTRALIA

**YOU CAN SET DRIFT FENCES IN THE CANOPY!**

Qualitative and quantitative methods exist for sampling the terrestrial herpetofauna in tropical rainforests. These include searching leaf litter in the businesses of trees (Inger 1980), forest litter plots (Scott 1976, 1982), and setting drift fences with pit and funnel traps (Vogt and Hine 1982). However, no one has developed a technique for systematically sampling herpetofauna in the canopies of tropical rainforests. A large percentage of the tropical herpetofauna is arboreal and many "rare" species may be so only because they are rarely encountered when sampling forest floors.

When discussing these problems with Dr. George Zug in December 1980 he could think of no solutions either, but replied: "You can't set drift fences in the canopy, Dick!" In 1981 after several aborted attempts, a convenient and inexpensive design (Fig. 1) was developed which catches reptiles and amphibians systematically at different strata of the forest canopy. The main feature is a system of four pulleys, a pair of which is attached to the two highest parallel branches 15 m apart on two trees. A 1 cm diameter nylon rope is threaded through each of the pulleys. Attached at various distances on the rope are "walkways" made of plastic window screening. The 0.9 cm-wide screening is cut in 15 m lengths. Galvanized wire is then threaded along the entire length on both edges of the screening and a length inserted crosswise at 1 m intervals to give support and maintain the shape of the "walkway." A 1 in length of 5 mm steel rod is tied at each end of the screening.

Harp Review 18(1), 1987

13
APPENDIX 3

CROCODYLUS JOHNSTONI IN THE McKinlay River Area, N.T.

VII. A POPULATION SIMULATION MODEL
**Crocodylus johnstoni** in the McKinlay River Area, N.T. VII*. A Population Simulation Model

Anthony M. A. Smith\textsuperscript{AB} and Grahame J. W. Webb\textsuperscript{AC}

\textsuperscript{A} Conservation Commission of the Northern Territory, P.O. Box 38496, Winnellie, N.T. 5789.
\textsuperscript{B} Department of Population Biology, Research School of Biological Sciences, The Australian National University, P.O. Box 475, Canberra City, A.C.T. 2601.
\textsuperscript{C} School of Zoology, University of New South Wales, P.O. Box 1, Kensington, N.S.W. 2033.

Abstract

A population simulation model was constructed for the McKinlay River population of the freshwater crocodile *Crocodylus johnstoni*. *C. johnstoni* are long-lived reptiles (50 y+) which take 9–16 years to reach maturity. As a consequence, the effects of legal hunting before 1963 are still reflected in an unstable population age structure. No quantitative data on the original population densities exist, nor are there data on the densities at which equilibrium can be expected in the future. The model examines the dynamics of a population which is still expanding and does not take into account density-dependent factors which may ultimately limit the population. If the population was undisturbed for 10 years, the model predicted the mean natural rate of population increase would be 1–5% per annum. However, the population has been disturbed during research activities, and when these disturbances and manipulations were simulated the model predicted a 4% decrease in the population between 1979 and 1983. Independent surveys in both 1979 and 1983 indicated a 5% decrease in the population. This consistency has been interpreted as indicating that the model's predictions are not grossly erroneous. Sensitivity tests were carried out in which most parameters in the model were independently varied by plus or minus their estimated error, while other parameters were held constant. The resultant changes in the estimated population size after 10 years indicated the model was most sensitive to the age-specific mortality estimates. *C. johnstoni* management has the conservation requirement of maintaining or even enhancing the density of wild populations. Sustained-yield harvesting can theoretically be achieved without compromising this requirement by harvesting eggs and/or hatchlings, and later returning a proportion of the harvest to the population when they are larger and have a greater probability of surviving. When released into the wild, captive-raised *C. johnstoni* survive as well as wild ones of equivalent sizes. The model was used to simulate egg and hatchling harvests with different collection and return rates, and different ages of returned animals. It was also used to simulate harvests of post-hatchling crocodiles, without a return of captive-raised animals.

Introduction

The endemic Australian freshwater crocodile, *Crocodylus johnstoni*, occurs in the northern parts of Western Australia, the Northern Territory and Queensland (Worrell 1964; Cogger 1979). In all three states populations were reduced during a period of commercial exploitation, particularly in the early 1960s (Bustard 1969, 1971). Protection (Western Australia, 1962; Northern Territory, 1963; Queensland, 1974) and the imposition of a total export ban (1972) has reversed this trend (Webb et al. 1983a).

In this study we incorporate life-history parameters derived by Webb and Smith (1984) and Webb et al. (1983a–1983f) into a population simulation model which is similar to that formulated for *Alligator mississippiensis* by Nichols et al. (1976b). The model is simplified in that it relies on constant parameter values (a mechanistic model). We use the model to attempt to:

1. Predict current recovery rate of the population (predictions are compared with data on the real recovery rate);
(2) Determine the magnitude of variation in the estimated recovery rate which could be expected from errors in the parameter values used;
(3) Examine four sustained-yield harvesting strategies which could be incorporated into a C. johnstoni management program: egg collection compensated for by a return to the population of a proportion of captive-raised juveniles (Blake 1974; Blake and Loveridge 1975); hatchling collection similarly compensated for; a random harvest of animals ≥2 years of age (Palmisano et al. 1973); and a random harvest of animals ≥1.5 m total length.

In reality, the effects of harvesting can only be quantified by field trials, which have been initiated. However, given the longevity of C. johnstoni and the long time it takes to reach maturity, egg and hatchling harvests may need to be carried out for many years before their effects are reflected in the adult population.

The extent to which density-dependent mechanisms are involved in population dynamics of C. johnstoni is unknown. Egg and hatchling survivorship are the most likely parameters affected, the former through females excavating other nests when laying their own eggs (Webb et al. 1983d) and also through some females nesting in areas with poor survivorship characteristics, i.e. those prone to excessive temperatures or with a high probability of flooding (Webb and Smith 1984). Hatchling survivorship is likely to be affected by density-dependent predation. These effects have not been quantified and no attempt has been made to incorporate them into the model.

Table 1. Mean parameter values, the type of estimates, error values and the type of error for all parameters used in the model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Type</th>
<th>Error (±)</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size</td>
<td>13.2</td>
<td>BME</td>
<td>0.34</td>
<td>SE</td>
</tr>
<tr>
<td>Hatching sex ratio</td>
<td>0.39</td>
<td>BME</td>
<td>0.03</td>
<td>SE</td>
</tr>
<tr>
<td>Female age at partial maturity</td>
<td>9</td>
<td>BPE</td>
<td>1</td>
<td>MLR</td>
</tr>
<tr>
<td>Female age at full maturity</td>
<td>12</td>
<td>BPE</td>
<td>1</td>
<td>MLR</td>
</tr>
<tr>
<td>Proportion of partially mature females breeding</td>
<td>0.286</td>
<td>BPE</td>
<td>0.10</td>
<td>MLR</td>
</tr>
<tr>
<td>Proportion of fully mature females breeding</td>
<td>0.844</td>
<td>BPE</td>
<td>0.10</td>
<td>MLR</td>
</tr>
<tr>
<td>Egg survivorship</td>
<td>0.295</td>
<td>BE</td>
<td>0.15</td>
<td>MLR</td>
</tr>
<tr>
<td>Hatchling survivorship</td>
<td>0.12</td>
<td>BE</td>
<td>0.05</td>
<td>MLR</td>
</tr>
<tr>
<td>Survivorship, years 1–10</td>
<td>0.85</td>
<td>BME</td>
<td>0.06</td>
<td>SE</td>
</tr>
<tr>
<td>Survivorship, years 11–30</td>
<td>1.000</td>
<td>BE</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Survivorship, years 31–50</td>
<td>0.86</td>
<td>BE</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Age at death</td>
<td>50</td>
<td>BE</td>
<td>10</td>
<td>MLR</td>
</tr>
</tbody>
</table>

Population Biology and Reproduction in McKinlay River C. johnstoni: a Review of Estimates Used in the Model

Parameter Values and Errors

The parameter values used in the model ranged from quantified means with calculated standard errors to informed guesses with likely ranges of error. To discriminate between the types of parameter values and their errors, the following terminology was adopted:

Best Mean Estimate (BME). A parameter mean empirically derived from field data, which has a calculated standard error (SE).

Best Point Estimate (BPE). A value derived once from field data but with no replicates to derive a SE.

Best Estimate (BE). A value derived secondarily from BMES, BPEs or other data, and which does not have a SE.

Most Likely Range (MLR). Where no SE has been calculated, available data have been used to guess a 'reasonable' error range.

The magnitude and type of all mean and error estimates are summarized in Table 1.
The Population Size and Age Structure

The method used for estimating the age of *C. johnstoni* relied on growth rates (Webb et al. 1983a). The age of younger animals can be predicted with reasonable accuracy, but for older animals, insufficient data are available to fully evaluate errors. Given that most of the population changes occurred in the younger year classes, minor errors in the age structure of older animals are unlikely to greatly affect the model's long-term predictions. However, given that less confidence can be held in the aging of older animals, the estimated age structure of recaptured animals greater than 10 years old in 1979 (Fig. 1a) has accordingly been smoothed (Fig. 1b), i.e. the numbers of animals in those age classes have been averaged.

![Figure 1](image_url)

**Fig. 1.** (a) The age structure of recaptured McKinlay River *C. johnstoni*. (b) Age structure simplified for modelling. The right-hand axis extrapolates the age structure to the total population.

Because the aging method could only be applied to recaptured animals (*n* = 240), the earliest cohort defined was 2-year-olds (y-o.). The number and sex ratio of 1-y-o.s was predicted from information given in Webb and Smith (1984) (*n* = 33; males, 7; females, 26).

![Figure 2](image_url)

**Fig. 2.** Age-specific survivorship of *C. johnstoni* eggs (modified from Webb and Smith 1984).

The animals represented in the age structure (*n* = 273) account for 28% of the estimated total population size. Capture methods (mostly fine nets; Webb and Messel 1977) were random with respect to the size and age of most crocodiles caught (exceptions 1-y-o.). Recapture rates were the same for both males and females, and emigration and immigration appeared negligible (Webb et al. 1983a, 1983b).

The total population in 1979 was estimated as 963 (likely range 826–1156; see Webb et al. 1983a) and its proportional age structure is on the right axis of Fig. 1a (Appendix 1). Because cohort sizes were rounded to integers, the total population estimate decreased to 957 individuals.
The population was extensively harvested between 1960 and 1963 and the size of the original population in the late 1950s is unknown, although from discussions with hunters we estimate a total of some 2000 individuals. Given that the population may not be at equilibrium density, the age structure may still be unstable and consequently a life table cannot be constructed from the population age structure per se (Caughley 1977).

**Age-specific Survivorship**

Webb and Smith (1984) derived an age-specific survivorship curve for post-protection cohorts (Fig. 2) ($y = 0.0505 \exp(-0.1632x)$, $r^2 = 0.75$, $n = 15$; where $y$ is the proportion of the cohort surviving and $x$ is age in years). The curve accounts for 75% of the variation, and multiple regression analysis attributed a further 17% of the variation to environmental conditions existing in consecutive incubation periods (Webb and Smith 1984). For example, the large 9-y-o. cohort (Fig. 1) resulted from a year with optimal rains for survivorship at the end of the incubation period. If the same conditions had existed for the 2-y-o. cohort (Fig. 1), a 2.5-fold increase in cohort size would have been expected.

(i) **Eggs to hatchlings**

Egg-laying occurs in August–September (dry season) with hatching (November–December) coinciding with the normal start of wet season rains. Predation, overheating, infertility and inundation reduce egg survivorship (Webb et al. 1983d, Webb and Smith 1984). An initial estimate of a 64% loss of eggs to predators (Webb et al. 1983d) could be inflated by our nest interference having enhanced predation (Deitz and Hines 1980). Losses to predators in 1982 and 1983, when access to eggs was restricted (Webb and Smith 1984), were 29% and 26%, respectively. A 50% loss of eggs to predators was considered a more realistic mean estimate, and as predators usually take all eggs within a nest, this represents a loss of 50% of nests.

Of the eggs not taken by predators in 1982 and 1983, 59% ± 12% (SE) produced apparently normal, healthy hatchlings. Therefore, of all eggs laid a BE of 29.5% (59% of 50%) can be expected to produce healthy hatchlings. Guessing that losses of eggs to predators are likely to vary ±10%, and that egg survivorship has a SE of ±12%, an MLR of ±15% was considered a realistic error range for the mean egg survivorship estimate of 29.5%.

(ii) **Hatchlings to one year of age**

Hatchling mortality is substantial and occurs mainly during the first wet season. By June, 2 months after the end of the wet season, there is a general paucity of hatchlings (Webb et al. 1983a, 1983d). The estimate used in the model is a mean of two independent estimates: the only ones available.

Firstly, on the basis of recapturing marked hatchlings, it was estimated that about 2% survived the first wet season (Webb et al. 1983d). Additional recaptures from the same experiment (unpublished data) indicated that 7.3% survived, but survivorship is patchy. In one pool, 45% of hatchlings released survived to 4 y o., which would mean that about 75% released in that pool had survived their first wet season.

Secondly, age structure analysis (Webb and Smith 1984) indicated that about 5% of eggs laid were represented as 1-y-o. survivors. If the estimate for average egg survivorship (29.5%) is applied, it indicates 17% hatchling survivorship to 1 y o.

The BE used in the model is 12% (the mean of 7% and 17%), and the MLR is ±5%; the actual range of the estimates.

(iii) **One to ten years of age**

The survivorship curve did not include 1-y-o.s, so we have assumed that extrapolation (dashed curve; Fig. 2) would adequately account for them (5% of eggs surviving to 1-y-o.s). The curve indicates approximately 85% annual survivorship between each subsequent year (BE) with an SE of ±6%. The SE is the standard error of the slope of the survivorship curve of Webb and Smith (1984).

(iv) **Eleven to thirty years of age**

If the survivorship curve for younger animals (Fig. 2) is extrapolated beyond 10 years, it indicates less than 0.5% survivorship by 16 years, yet clearly a substantial number of animals do survive (Fig. 1). We have interpreted this as an indication that once the age of about 10 y o. is reached, annual mortality is negligible for a number of subsequent years. From the age structure (Fig. 1a) there is no evidence for significant mortality between 11 and 30 years. For the purposes of the model, we have assumed negligible mortality (100% survivorship; a BE) between 11 and 30 years of age. No reasonable error for this estimate could be derived.
Crocodylus johnstoni in the Northern Territory. VII

30 to fifty years of age

The maximum age attainable by C. johnstoni is poorly known. One individual was estimated as being 43 years of age in 1979 on the assumption of minimal growth when in fact, none had occurred over 2 years (Webb et al. 1983a). We have assumed 50 years as a BE and, during model operation, any animal reaching 50 y.o. dies. It has been assumed that 5% of animals reaching 31 y.o. will eventually reach 50 y.o., and that survivorship between 31 and 50 y.o. is exponential, 86% survivorship per year (BE).

As survivorship after 31 years is derived directly from an assumed age at death, errors cannot be reasonably derived for each as an independent parameter. Therefore, if an MLR of ±10 years is accepted for age at death, survivorship after 31 years is calculated on that basis, i.e., if age at death is 40 years, then survivorship is calculated by assuming that 5% of animals reaching 31 y.o. will survive to 40 y.o.

Survivorship of Captive-raised Animals Returned to the Wild

In late 1981, 34 captive-raised 1-y-o. C. johnstoni (Webb et al. 1983c) were released into three pools in the downstream section of the McKinlay River. Six months later, the pools were surveyed with spotlights and an attempt was made to catch all C. johnstoni of the appropriate size class. Six of the 34 were recaptured, all in the same pools in which they had been released. One year after release, crocodiles in the three pools were caught with fine nets (Webb and Messell 1977) and six of the released animals were recaptured, two of which had also been recaptured after 6 months.

Webb et al. (1983a) recaptured 39% of wild marked crocodiles of this size class after 1 year, and 72.8% of all animals recaptured were in the same pools in which they had been released. Disregarding a tendency for young animals to move more than older ones, about 28% of wild-released 1-y-o.s could be expected to be recaptured in the same pool 1 year later. Neither the total number recaptured (n = 6; 18%), differed significantly from the expected retrieval ($\chi^2 = 0$, $P > 0.90$; $\chi^2 = 1.31$, 0.25 > $P > 0.10$ respectively). The model assumes that released captive-raised animals would survive as well as wild ones of the same age.

Reproductive Biology

Females can mature at 9 y.o. (BPE: ± 1 y, MLR) but 12 y.o. (BPE: ± 1 y, MLR) is the estimated average age (Webb et al. 1983d). Males mature later, 16 y.o. being estimated as the average age (Webb et al. 1983a, 1983d).

Age of reproductive senescence is unknown. The oldest female was 43 y.o. in 1979 and was recaptured in 1980, but not in 1982. An age of 45 y.o. was considered a reasonable estimate, 5 years before death. Males do not appear to be limiting in the population and an estimate is not required for the model. However, one testis of a large male examined was regressing (Webb et al. 1983a) and reproductive senescence probably precedes death, as in C. niloticus (Graham 1968) and A. mississippiensis (Ferguson 1985).

C. johnstoni nest once a year, and 28-6% (BPE: ± 10%, MLR) of females between 9 and 11 years of age nest annually (partial female maturity). Of females ≥12 years of age, 54.3% (BPE: ± 10%, MLR) nest annually (full female maturity), an estimate which takes account of senescent females (Webb et al. 1983a, 1983d). Although clutch size probably increases for a time with female age and size (Ferguson 1985), the relationship has not been quantified and has accordingly been ignored in this model. Mean clutch size in the McKinlay River area is 13.2 (BME: ± 0.34, SE), with the largest eggs (older or bigger females?) ranging from 4 to 19 per clutch and the smallest eggs from 5 to 13 per clutch (Webb et al. 1983d).

Hatching Sex Ratio

Sex determination in embryonic C. johnstoni is dependent on the environment in which the eggs are incubated, particularly temperature (Webb et al. 1983d, Webb and Smith 1984). The sex ratio of cohorts varies widely, and has been less than 0.5 (expressed as the proportion of males) since protection. Annual hatching sex ratio is highly correlated with water height at the time of nesting (August), probably because water height influences the availability of nest sites with different thermal characteristics (Webb and Smith 1984). However, hatching sex ratios are also modified by differential mortality between the sexes, partly dependent on the extent of rains (and flooding) at or near hatching (Webb and Smith 1984). On the basis of mean August water heights between 1959 and 1981, mean hatching sex ratio has been estimated as 0.39 (BME: ± 0.03, SE) (1 male to 1.56 females). The sex ratio of immature C. johnstoni caught in the McKinlay River area is 0.36 (Webb and Smith 1984).
The Model

General

The model was constructed around two 1 by 50 population vectors, with each vector element representing a year class for a particular sex. The initial population was that from the McKinlay River in 1979, modified as described (Fig. 1). The model operated one year at a time and mortality occurred as a single event at the end of each wet season.

During operation all year classes were multiplied by the relevant survivorship proportions (1–10 y.o., 0.849; 11–30 y.o., 1.000; 31–50 y.o., 0.861). The number of breeding females in any year was determined by applying age-specific breeding proportions (0–8 y.o., 0.000; 9–11 y.o., 0.286; 12–50 y.o., 0.844), and the number of eggs by applying clutch size (13.2 eggs). The number of hatchings and 1-y.o.s was derived by applying the egg survivorship proportion (0.295) and the hatchling survivorship proportion (0.12) respectively. One-year-olds were allocated to the vectors on the basis of a 0.39 sex ratio (39% males).

Parameter Values and Errors

Parameter values are a combination of estimates with calculated or guessed errors. Because the influence of these errors on the estimated population size after 10 years would differ between parameters, sensitivity simulations were accordingly undertaken. The estimated total population after 10 years was determined with each parameter at its standard value minus one SE (or MLR) and its standard value plus one SE (MLR). For each sensitivity test, the value of only one parameter was altered; all others were held at their standard value.

Harvest Strategies

Implicit within the egg and hatchling harvests simulated are the existence of crocodile farms, in which eggs are artificially incubated and hatchlings raised until of a commercially acceptable size.

The egg harvest was simulated by removing eggs from the population before they hatched, storing them on a farm, and returning a proportion to the wild as raised post-hatchlings of varying ages. In the simulations, nested loops were constructed whereby 0–100% (in 10% increments) of all eggs laid were collected. For each collection rate, 0–100% of post-hatchlings were returned to the wild at 1, 3, and 5 years of age. Hatchling collection and the return of 1, 3 and 5-y.o.s was achieved in the same manner and with the same increments. Each combination of collection rates, return rates and ages of return was maintained for 10 consecutive years, yielding a total harvest (of eggs or hatchlings) and a final wild harvested population size ($JIP_{10}$). The impact of each combination tested was assessed by comparing the $JIP_{10}$ with the standard population estimate after 10 years ($STP_{10}$), which simulates total protection. If the $JIP_{10}$ and $STP_{10}$ were the same, the harvest strategy was interpreted as having no impact on the recovery rate of the wild population. Theoretically, the natural recovery rate of a population can be enhanced by various combinations of collection rate, return rate and ages of return, although clearly this assumes that no density-dependent factors are currently limiting the population.

A hunting subroutine harvested animals $\geq 2$ y. The population was harvested annually in 1% increments up to 10%; no attempt was made to compensate for the harvest by restocking the wild. The harvest was applied equally to both sexes and to all age classes. The same routine was used to simulate an annual harvest of 1–10% of animals $\geq 1.5$ m total length (males $\geq 12$ y.o.; females $\geq 14$ y.o.). In both cases the $HP_{10}$ and $STP_{10}$ were compared to assess the impact of the harvest.

Chronology of Model Operation

The model begins its cycle in the middle of the dry season when the crocodiles breed. Eggs are laid and are harvested if specified. The remaining eggs in the wild then hatch and hatchlings are harvested if specified. The wet season follows and with it all annual mortality. The following
dry season is entered and any animals collected as eggs or hatchlings that have reached their return age are returned to the population. Hunting, if it takes place, directly follows the return of animals to the wild and precedes the second breeding season.

Testing the Model's Predictions
In July 1979, 505 C. johnstoni were sighted during spotlight surveys throughout the total McKinlay River study area (Webb et al. 1983e). Between 1979 and 1983, 2026 eggs were collected (18.4% of the estimated production per year) and 30 animals of different ages were killed or removed. Simultaneously, 71 hatchlings, 79 6-month-old animals and 34 1-y-o.s were released into the system.

![Graph showing predicted population growth](image)

Fig. 3. Predicted increases in the McKinlay River C. johnstoni population over 30 years.

The model was programmed to simulate the manipulations and to generate an estimate of the total population size in 1983. This estimate was compared with the results of a 1983 spotlight survey of the areas which contained 77.2% of the population in 1979. Survivorship from 0.5 to 1 y.o. needed to be estimated and the mean of that from hatching to 1 y.o. (12%) and that from 1 to 2 y.o. (85%) was used (48.5%).

The comparison assumes that the counts include a random proportion of the population, which may not be strictly valid. However, an estimated 50–70% of crocodiles present are seen in such surveys (Webb et al. 1983e). Thus, the surveys included 41% of the total population.

Results

Population Growth Rate
The model indicated that the population would increase exponentially over the next 10 years (Fig. 3) and would then undergo a period of linear growth. This period of linear growth (30 years) is due to the stabilizing of the age structure. Once this is achieved, the population again increases exponentially (not shown in Fig. 3), because the model does not contain density-dependent factors, and the sex ratio of recruits is biased to females. This second exponential growth may have little relevance to what will occur in the field in 30 years time, as food, space and access to suitable nest sites could all function to limit population growth. Mean annual population growth rates were predicted as 1.5, 2.0 and 1.9% for 10-, 20- and 30-year periods respectively. Growth rates between consecutive years ranged from −1.4% (years 0–1) to 3.4% (years 8–9). This variation reflects the differences in the sizes of the first 10 year classes (Fig. 1).
Predicted changes in the age structure are shown in Fig. 4. When only adult females are considered, mean annual population growth rates were 3.1%, 2.5%, and 2.1% for 10-, 20-, and 30-year periods respectively.

Testing the Model’s Predictions

The model predicted the total population in 1983 should be 939 individuals, 96.0% of the 1979 population. Spotlight counts in July 1983 yielded 369 sightings in an area which previously yielded 390 (94.6%; July 1979). This result could be fortuitous and it could have been derived by processes quite different to those modelled. However, given the high proportion of the total population included in the survey (about 40%), the result is consistent with ‘low’ rates of population increase.

Parameter Values and Errors

The SES and MLRs of the parameters introduced errors ranging between 0 and 57.6% in the estimated population size after 10 years (Table 2; ranked from 1 to 10 on the basis of the magnitude of the error resulting from the SE or MLR). Although the use of these results to ascribe ‘relative importance’ to each parameter may be misleading, the results do serve as indicators of probable sources of error. For example, the MLR of egg survivorship generates the greatest error over
10 years. It is accordingly the parameter value which should be reconsidered first if the model's predictions were found to be in substantial error.

Table 2. The results of simulating the population with each standard value increased (PE+) or decreased (PE−) by its error

These new population estimates, when expressed as a function of STP10, indicate the sensitivity of the model to variation in the parameter estimates used

| Parameter                              | Value     | PE+   | PE−   | \(
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size</td>
<td>13.2 ± 0.34</td>
<td>1126</td>
<td>1093</td>
<td>3.0</td>
</tr>
<tr>
<td>Hatchling sex ratio</td>
<td>0.39 ± 0.03</td>
<td>1110</td>
<td>1110</td>
<td>0.0</td>
</tr>
<tr>
<td>Female age at partial maturity</td>
<td>9 ± 1</td>
<td>1126</td>
<td>1094</td>
<td>2.9</td>
</tr>
<tr>
<td>Female age at full maturity</td>
<td>12 ± 1</td>
<td>1136</td>
<td>1083</td>
<td>4.8</td>
</tr>
<tr>
<td>Proportion of partially mature females breeding</td>
<td>0.286 ± 0.10</td>
<td>1125</td>
<td>1095</td>
<td>2.7</td>
</tr>
<tr>
<td>Proportion of fully mature females breeding</td>
<td>0.844 ± 0.10</td>
<td>1179</td>
<td>1040</td>
<td>12.5</td>
</tr>
<tr>
<td>Egg survivorship</td>
<td>0.295 ± 0.15</td>
<td>1430</td>
<td>791</td>
<td>57.6</td>
</tr>
<tr>
<td>Hatching survivorship</td>
<td>0.12 ± 0.05</td>
<td>1372</td>
<td>848</td>
<td>47.2</td>
</tr>
<tr>
<td>Survivorship, years 1–10</td>
<td>0.85 ± 0.06</td>
<td>1435</td>
<td>880</td>
<td>50.0</td>
</tr>
<tr>
<td>Survivorship, years 11–30</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Survivorship, years 31–50</td>
<td>0.86</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Age at death</td>
<td>50 ± 10</td>
<td>1150</td>
<td>1036</td>
<td>10.3</td>
</tr>
</tbody>
</table>

Harvest Strategies

(i) Egg and hatchling collection

The relationship between collection and return rates, of 1-, 3- and 5-y-o. animals, is summarized in Tables 3 (eggs) and 4 (hatchlings).

Table 3. The results of simulated egg harvests: the population size after 10 years, given various collection and return rates

Values in parentheses are animals still to be released by farms and the number of animals retained by farms respectively. The initial population size was 957 individuals, and without harvesting this would increase to 1110

<table>
<thead>
<tr>
<th>Return rate (% of eggs collected)</th>
<th>Age of returned animals (y)</th>
<th>Collection rate (percentage of total egg population)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>—</td>
<td>1047 (0; 3143); 796 (0; 15706); 546 (0; 28249)</td>
</tr>
<tr>
<td>10</td>
<td>1</td>
<td>1224 (37; 2831); 1685 (188; 14172); 2147 (342; 25544)</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>1198 (108; 2831); 1552 (544; 14186); 1905 (986; 25590)</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>1170 (174; 2832); 1410 (873; 14206); 1647 (1581; 25654)</td>
</tr>
<tr>
<td>20</td>
<td>1</td>
<td>1402 (75; 2517); 2581 (384; 12630); 3775 (711; 22813)</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>1350 (217; 2518); 2309 (1099; 12655); 3264 (2008; 22895)</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>1293 (348; 2520); 2024 (1762; 12691); 2747 (3214; 23009)</td>
</tr>
</tbody>
</table>

In all simulations the initial population size was 957 animals and the STP10 was 1110 animals. HP10 below 1110 indicate the harvest would reduce the natural rate of population increase. Each combination of collection and return rates is represented by the HP10, the number of animals the farms are still to release (i.e. animals being raised until they reach their release age), and the extent of the harvest which the farms can use for their own purposes.
Values well above those that would be set for harvest are included, as the same strategies could theoretically be used to enhance population growth in areas where numbers are depleted.

Table 5 contains the full results from egg and hatchling harvests in which the $H_{P10}$ equals the $STP_{10}$. The following conditions were set for these two examples.

Table 4. The results of a simulated hatchling harvest: the population size after 10 years, given various collection and return rates

Values in parentheses are animals still to be released by farms and the number of hatchlings retained by farms respectively. The initial population size was 957 individuals and without harvesting this would increase to 1110

<table>
<thead>
<tr>
<th>Return rate (% of hatchlings collected)</th>
<th>Age of returned animals (y)</th>
<th>Collection rate (percentage of total hatchling population)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10</td>
<td>50</td>
</tr>
<tr>
<td>0</td>
<td>1047 (0; 927)</td>
<td>796 (0; 4633)</td>
</tr>
<tr>
<td>10</td>
<td>1099 (11; 835)</td>
<td>1057 (55; 4173)</td>
</tr>
<tr>
<td>3</td>
<td>1091 (32; 835)</td>
<td>1019 (159; 4174)</td>
</tr>
<tr>
<td>5</td>
<td>1083 (51; 835)</td>
<td>977 (256; 4176)</td>
</tr>
<tr>
<td>20</td>
<td>1151 (22; 742)</td>
<td>1319 (110; 3712)</td>
</tr>
<tr>
<td>3</td>
<td>1136 (64; 742)</td>
<td>1242 (320; 3714)</td>
</tr>
<tr>
<td>5</td>
<td>1119 (102; 742)</td>
<td>1158 (513; 3717)</td>
</tr>
</tbody>
</table>

Collection. That 50% of the total number of eggs and 90% of the total number of hatchlings were collected. In reality many variables affect these percentages, and although they are realistic for the McKinlay River and Finniss River area (Webb et al., unpublished data), they are not so in some other areas.

Hatching. That 70% of eggs located were successfully hatched. This percentage can be expected if eggs are collected, transported and incubated with care. Joanen and McNease (1977, 1981) achieved a 94% hatching rate of $A.\ mississippiensis$ fertile eggs (5.8% were infertile) and we now achieve better hatching success with $C.\ johnstoni$ eggs than previously reported (Webb et al. 1983d). Less than 4% of $C.\ johnstoni$ eggs are infertile and < 5% may be damaged by the probing technique used to locate nests (Webb et al. 1983d).

Table 5. The detailed results of an egg and hatchling harvest with returns, designed such that the wild population size equals the population size expected without any harvest after 10 years (1110)

<table>
<thead>
<tr>
<th>Egg collection</th>
<th>Hatchling collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at return (y)</td>
<td>1</td>
</tr>
<tr>
<td>Collection rate (%)</td>
<td>50</td>
</tr>
<tr>
<td>Maximum return rate possible (%)</td>
<td>60</td>
</tr>
<tr>
<td>Total harvest over 10 y</td>
<td>15 164</td>
</tr>
<tr>
<td>Return needed to balance natural population increase (%)</td>
<td>3.54</td>
</tr>
<tr>
<td>Population size after 10 y</td>
<td>1110</td>
</tr>
<tr>
<td>No. of animals still to be returned at end of 10 y</td>
<td>66</td>
</tr>
<tr>
<td>Total harvest less animals returned, or to be returned</td>
<td>14 627</td>
</tr>
</tbody>
</table>

First-year mortality. That 15% mortality occurs in the first year of life, both in farms and in the wild. This estimate approximates the mortality in two crocodile farms raising $C.\ johnstoni$ (<10%) at present.
Later mortality. That mortality after 1 year would be 5% per annum in the crocodile farms. This estimate approximates current losses.

When an egg collection with a return of 1-y-o.s is used as an example (Table 5), 50% of all eggs laid were collected each year for 10 years; 70% hatched and, with a mortality rate of 15%, 60% of the number of eggs collected were represented as 1-y-o.s. (If all these were returned to the wild each year and no density-dependent factors altered survival, the population would theoretically increase to 6268.) Altogether 15 164 eggs would have been collected. For the $HP_{10}$ to balance rather than exceed the $STP_{10}$, 3.54% of the number of eggs collected each year would need to be returned as 1-y-o.s (537 over 10 y), leaving a total harvest of 14 627 eggs which could be retained by the farms. The returns to the wild would need to continue for 1, 3 and 5 y after the 10-y period expired.

Table 6. The simulated effects of two random annual harvests applied to a *C. johnstoni* population of 957 individuals for 10 consecutive years

<table>
<thead>
<tr>
<th>Without hunting the final population size is estimated as 1110 individuals. The harvest restricted to animals $\geq 1.5$ m would include females $\geq 14$ y and males $\geq 12$ y</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population size after harvest of:</td>
</tr>
<tr>
<td>Total harvest</td>
</tr>
<tr>
<td>Population size after 10 y</td>
</tr>
<tr>
<td>Total harvest</td>
</tr>
<tr>
<td>Population size after 10 y</td>
</tr>
</tbody>
</table>

(ii) Proportional hunting

The proportional harvests of animals $\geq 2$ y and $\geq 1.5$ m was simulated for 10 years (Table 6) with a set proportion of animals being harvested from each age class. With no return to the wild included in the simulation, the $HP_{10}$ was always less than the $STP_{10}$.

Discussion

The 1.5% population growth rate predicted by the model was appreciably lower than that reported for *A. mississippiensis*, both from field surveys (16·9%; Joanen and McNease 1982) and from a simulation model (5·28%; Nichols et al. 1976b). This difference appears to be real and could be explained by differences in fecundity and age-specific survival: *A. mississippiensis* females lay three times as many eggs per annum, and both eggs and hatchlings appear to have a greater probability of surviving (Joanen 1969; Nichols et al. 1976b). These two factors alone give *A. mississippiensis* populations a greater potential to increase than those of *C. johnstoni*.

The extent to which the model's predictions reflect the real situation within and outside the McKinlay River is difficult to evaluate. The comparison of 1983 and 1979 spotlight counts were consistent with the model's predictions (low rates of population increase), but this may have been fortuitous. However, low rates of *C. johnstoni* population increase have also been found in Katherine Gorge National Park (Terry Bartlett, unpublished data). Over 3 years the population has remained stable, although monthly variation within any one year can be extreme. Counts of *C. johnstoni* in the Adelaide River (Webb et al. 1983f) indicate a significant decline in the population between 1979 and 1982, but this appears to be correlated with increasing numbers of *C. porosus* in the area.
Estimating the rate of population increase is a requisite to setting harvest levels (Caughley 1977) and this is particularly so with crocodilians. The management of crocodilians spans two of Caughley’s (1977) categories, in that it is desirable to enhance or maintain population density (conservation) and exploit the population (sustained-yield harvesting) simultaneously, as is done with *A. mississippiensis* in Louisiana (Joanen and McNease 1982). Strategies for maximizing a harvest are thus constrained by the conservation requisite. Hence a population 'manipulation-type' harvest of the type examined here appears the only acceptable option.

A low rate of *C. johnstoni* population increase indicates that a hunting harvest of the type currently applied to *A. mississippiensis* (Palmisano et al. 1973; Joanen and McNease 1982; Taylor and Neal 1984) could be directed at only a small proportion of the *C. johnstoni* population (Table 6), unless compensated for by a return to the wild of raised young (Nichols et al. 1976a). Such a harvest may not be an economical option unless the value of individuals removed could be greatly increased.

In contrast, an egg or hatchling harvest of the type carried out in Zimbabwe (Blake 1974; Blake and Loveridge 1975) appears to have considerable potential. If the model's predictions are correct, up to 30% of *C. johnstoni* eggs or hatchlings could be removed from a population annually. Even without any of these returned to the wild, the population should not be seriously affected. Indeed, 90% of hatchlings or eggs could be removed for 10 y and the population would only be halved, indicating that even the most extreme of the strategies presented here would not effect catastrophic changes in a population in the short term. If a proportion of the harvest was returned to the wild as raised juveniles, the total harvest which could be taken (Tables 3–5), while still maintaining the natural rate of population increase, would be greatly increased. Clearly, field trials are needed, because the model’s predictions assume an absence of density-dependent factors in population regulation.

The choice between an egg or hatchling harvest needs to be resolved, with data on the effectiveness with which large-scale harvests of both can be carried out. The following advantages and disadvantages would need to be considered (Joanen and McNease 1981; Ferguson and Joanen 1982, 1983; Webb et al. 1983d; Ferguson 1985; Webb and Smith 1984).

**Egg Harvest**

(i) **Advantages**

1. Egg-laying occurs in a contracted 3-week period in the dry season when many nesting areas are accessible by vehicle;
2. Colonial nesting is common;
3. At least 50% of eggs do not produce hatchlings if left in the field;
4. If eggs are collected at an early age and incubated with correct temperature and moisture conditions, high hatching rates (>80%) can be expected;
5. The number of eggs available for collection is more predictable than the number of hatchlings, because variation in incubation success in the field is negated;
6. Sex, and the amount of yolk which embryos hatch with, can be controlled by the incubation conditions.

(ii) **Disadvantages**

1. At least 9% of eggs found will not produce hatchlings: about 4% are infertile, and up to 5% may be damaged by the probing technique used to find them;
2. Mean clutch size is 13 eggs;
3. Eggs need to be found and transported when freshly laid to avoid losses to predators, and to minimize embryo losses due to mechanical shock during transportation;
4. Eggs must be incubated under controlled temperature and moisture conditions for 70–90 days.
Hatchling Harvest

(i) Advantages

(1) Risks of egg collection and incubation are avoided;
(2) In many areas hatchlings are relatively easy to locate and catch at night;
(3) Compared with eggs, hatchlings are robust and can readily withstand the physical stresses associated with collection and transportation.

(ii) Disadvantages

(1) Hatching occurs over a more prolonged period than does nesting;
(2) Hatching occurs at the start of the wet season. Early rains can restrict access to nesting areas and may cause catastrophic nest flooding (embryo mortality) in some years;
(3) Availability of hatchlings is less predictable than that of eggs because it is dependent on annual variation in egg survivorship.

By way of conclusion, we would like to emphasize that although models such as the one presented here are useful for predicting the possible outcome of specific harvest strategies, regardless of wide variation in prediction accuracy, one of their main values lies in the early detection of strategies which may have catastrophic consequences. Such a distinction is particularly important when the species being dealt with is one of a group whose conservation status has given cause for concern both nationally and internationally (Groombridge 1982).

Acknowledgments

Many people have assisted in the collection of the data which made this study possible, and we would particularly like to thank Rik Buckworth, Charlie Manolis, John Barker, Tony Spring, Karen Dempsey and George Sack. Les Mitchell provided advice on model implementation on the IBM 3032, and Robin Craig provided similar advice for the Cyber 7276. We would like to thank Bill Freeland and Peter Bayliss for critically reviewing various stages of the manuscript. Financial assistance came primarily from the Conservation Commission of the Northern Territory, with additional support from the University of New South Wales.

References


### Appendix 1. Simplified age structure of the McKinlay River *C. johnstoni* population

<table>
<thead>
<tr>
<th>Year class</th>
<th>Males</th>
<th>Females</th>
<th>Year class</th>
<th>Males</th>
<th>Females</th>
<th>Year class</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>25</td>
<td>92</td>
<td>18</td>
<td>5</td>
<td>9</td>
<td>35</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>35</td>
<td>49</td>
<td>19</td>
<td>5</td>
<td>9</td>
<td>36</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>35</td>
<td>42</td>
<td>20</td>
<td>5</td>
<td>9</td>
<td>37</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>32</td>
<td>74</td>
<td>21</td>
<td>1</td>
<td>9</td>
<td>38</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>5</td>
<td>39</td>
<td>46</td>
<td>22</td>
<td>1</td>
<td>9</td>
<td>39</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>6</td>
<td>18</td>
<td>42</td>
<td>23</td>
<td>1</td>
<td>9</td>
<td>40</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>7</td>
<td>14</td>
<td>28</td>
<td>24</td>
<td>1</td>
<td>9</td>
<td>41</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td>7</td>
<td>11</td>
<td>25</td>
<td>1</td>
<td>9</td>
<td>42</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>7</td>
<td>53</td>
<td>26</td>
<td>1</td>
<td>9</td>
<td>43</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>10</td>
<td>4</td>
<td>14</td>
<td>27</td>
<td>1</td>
<td>9</td>
<td>44</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>5</td>
<td>9</td>
<td>28</td>
<td>1</td>
<td>9</td>
<td>45</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
<td>5</td>
<td>9</td>
<td>29</td>
<td>1</td>
<td>9</td>
<td>46</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>13</td>
<td>5</td>
<td>9</td>
<td>30</td>
<td>1</td>
<td>9</td>
<td>47</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>14</td>
<td>5</td>
<td>9</td>
<td>31</td>
<td>1</td>
<td>3</td>
<td>48</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>15</td>
<td>5</td>
<td>9</td>
<td>32</td>
<td>1</td>
<td>3</td>
<td>49</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>16</td>
<td>5</td>
<td>9</td>
<td>33</td>
<td>1</td>
<td>3</td>
<td>50</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>17</td>
<td>5</td>
<td>9</td>
<td>34</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Manuscript received 23 July 1984; accepted 10 April 1985