THE MURRAY RIVER TURTLE, *Emydura macquarii*:



POPULATION DYNAMICS, NESTING ECOLOGY AND IMPACT OF THE INTRODUCED RED FOX, Vulpes vulpes

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STATEMENT OF RESPONSIBILITY

This thesis is my original work, except where specifically acknowledged

find 1

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July 2000

The First Turtle

In the early days of the Dreamtime there lived a man called Mungi. Mungi was a well known entertainer. One day Mungi was invited to go and entertain a group who lived on a small island. Mungi could not swim so the two best hunters from the group helped him across to the island. Mungi entertained the people there for several weeks and they were pleased that he was staying with them. But soon he wanted to leave. The two men who had brought him to the island did not want to leave and if Mungi tried to escape he would be killed by them.



Christopher Prentice

Mungi was shocked! He broke his clap sticks on purpose and told his captors that to make some more clap sticks, he needed wood from a certain tree only found on the mainland. The two hunters went across and got a log for him. Mungi told them that the log needed to be left overnight before he could start making the clap sticks.

That night Mungi used the log to try and get across to the mainland. But he was in the hollow of the log and could only use his arms and legs, so he could not go very fast, nor go very far. Before long the two hunters awoke and started throwing their spears at Mungi. As long as he kept his arms and legs inside the log he was safe. But when he stuck his head out to see if he was getting closer to shore, the hunters saw him. One of them threw his spear and struck Mungi in the neck. He thought he was going to die. But his ancestor spirits were watching too and their magic saved his life. But he wasn't quite the same for when he reached shore, he discovered he had changed. He was a new animal able to live on land and in the sea and also had a hard protective shell on his back.

Mungi had become the very first turtle.

An aboriginal Dreamtime story, reproduced at http://www.cltr.uq.oz.au/~bardonm/

Abstract

I studied aspects of the ecology of the Murray River turtle, *Emydura macquarii*, to determine the impact of the introduced red fox, *Vulpes vulpes*. The fox is one of Australia's worst vertebrate pests through its predation on livestock and native mammals, but their impact on reptilian communities is not known.

I conducted a large-scale mark-recapture study to evaluate population growth of *E. macquarii* in the Albury region of the upper Murray River by determining growth, reproduction and survival. The study was conducted downstream of the first, and largest, impoundment on the Murray River, Lake Hume. *Emydura macquarii* predominantly inhabit the lagoons in the upper Murray River, as the mainstream and Lake are possibly too cool to maintain metabolic processes. They are easily captured in hoop traps and the use of live decoys maximises trap success.

Over 2000 hatchling turtles were marked and released into two lagoons between January 1997 and January 1998. Growth of these individuals is rapid over the first few years but declines towards maturity, and is indeterminate after maturity. Although growth annuli are not well defined, even on young individuals, the von Bertalanffy model describes the growth of both male and female *E. macquarii*. Male turtles mature at 5-6 years and females mature at 10-12 years. Female turtles may maximise reproductive potential by delaying maturity and producing one relatively large clutch (mean = 21 eggs) per year, i

which is positively correlated with body size (PL). Although primarily related to body size, clutch size varies annually because of environmental conditions. If winter and summer rainfalls are below average and temperatures are above average, *E. macquarii* may reduce clutch size to increase the chance of the eggs surviving.

Nesting predominantly occurs during the first major rain-bearing depression in November. Habitat variables, including distance from water, nearest nest, and tree, and soil type were measured for each nest to determine characteristics that attract predators. Nests close to the shoreline and trees are heavily preyed on, and nests constructed in sand are less likely to be destroyed by predators. Foxes detect nests through a combination of chemical cues from eggs and slight soil disturbances, whereas birds only destroy nests observed being constructed during the day.

Female turtles alter nesting behaviour and construct nests much further away from water when foxes were removed and as a result, nests are less dense and away from trees. Thus in high predation risk areas, turtles minimise emergence and search times to reduce the risk of direct predation by foxes. Predation is reduced when nests are in lower densities and away from trees, because predators increase search efforts when nests are in higher densities and birds are more likely to destroy nests close to trees. Reproductive success is further reduced in high predation risk areas because more nests are constructed in sandy substrates where clutch success is reduced compared to incubation in more dense substrates. Where predators are a significant source of mortality, prey may use indirect methods, such as chemical recognition, to avoid encounters. Nesting turtles did not avoid areas where fox odour was present, suggesting that they assess predation pressure from foxes by other mechanisms, such as visual recognition. However, an innate response occurs to the odour of a once common predator on the Murray River, the eastern quoll (*Dasyurus viverrinus*), whereby turtles recognise and avoid nesting in areas where quol odour is present. Therefore nesting turtles show a similar avoidance response to two different predators, using different mechanisms of detection. Similarly, predation risk may influence hatching times and nest emergence. The rate of embryonic development of *E. macquarii* may increase or eggs may hatch early so that the clutch hatches synchronously, thereby reducing the risk of predation through group emergence from the nest.

Emydura macquarii reach densities of over 100 turtles.ha⁻¹, with the majority of the population consisting of sexually mature individuals. *Emydura macquarii* has a Type III survival curve where mortality is extremely high in the egg stage (<90% nest predation), remaining high over the hatchling stage (minimum survival rate- 10%), but decreasing rapidly throughout the juvenile stage (~70% juvenile survival). Adult survival is extremely high, with greater than 95% of adults surviving each year. Foxes through nest predation cause most mortality but a small proportion (~3%) of nesting adult females are

killed by foxes each year. A removal program evaluated the impact of foxes. In 1996, fox numbers were monitored around four lagoons by spotlighting and non-toxic bait uptake. Foxes were removed from around two of the lagoons throughout 1997 and 1998, using spotlight shooting and 1080 bait poisoning. Fox numbers were continually monitored around all four lagoons during the study. Nest predation rates remained around 90% in all sites where foxes were present, but fell to less than 50% when foxes were removed. At the same time, predation on nesting female turtles was eliminated where foxes were removed.

Demographic models using staged based survival schedules, together with growth and fecundity values for *E. macquarii* show a decline of 4% per year in these populations. Elasticity analyses shows that survival of adult female *E. macquarii* has the major influence on population stability and a reduction of nest predation alone is unlikely to address the population decline. Management options, such as reducing foxes prior to nesting around key lagoons, will stabilise the population decline, and eliminating foxes completely from certain areas with high dispersal potential, will promote recruitment of juvenile *E. macquarii*.

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| Table of Contents | |
|---|----------|
| Abstract | i |
| Acknowledgements | iv |
| TABLE OF CONTENTS | vi |
| CHAPTER 1: GENERAL INTRODUCTION | 1 |
| 1.1 MURRAY RIVER TURTLES | 2 |
| 1.1.1 Emydura macquarii: The Murray Short-Neck Turtle | 4 |
| 1.2 THE RED FOX IN AUSTRALIA AND THE INTRODUCTION OF GENERALIST VERTEBRATE PREDATORS | 6 |
| 1.3 THE ROLE OF <i>E. macquarii</i> IN THE MURRAY RIVER | 9 |
| 1.4 EVALUATING POPULATION DECLINES | 10 |
| 1.5 AIMS AND SCOPE OF THE THESIS | 14 |
| CHAPTER 2: STUDY SITES AND METHODS | 16 |
| 2.1 STUDY SITES | 16 |
| 2.1.1. Location | 16 |
| 2.1.2. Vegetation | 18 |
| 2.1.3. Climate | 18 |
| 2.1.4. Lagoon Habitat | 20 |
| 2.1.5. Hawksview | 24 |
| 2.1.6. Bankview | 26 |
| 2.1.7. Snowdon's | 21 |
| 2.1.0. COOKS 2.1.9. Mulwala lagoon | 20 29 |
| 2.1.10. Lake Mulwala | 29 |
| 2.2 TURTLE CAPTURE | 31 |
| 2.2.1. Hoop traps and other capture methods | 31 |
| 2.2.2. Captured turtles | 32 |
| 2.2.3. Egg collection, incubation and hatchlings | 33 |

| CHAPTER 3: DISTRIBUTION OF TURTLES AND DEVE | LOPMENT OF |
|---|------------|
| CAPTURE TECHNIQUES | |

| 3.1 INTRODUCTION | 35 |
|--|----|
| 3.2 MATERIALS AND METHODS | 37 |
| 3.2.1. Habitat and Distribution | 37 |
| 3.2.2. Maximising Trap Success | 38 |
| 3.3 RESULTS | 39 |
| 3.3.1. Habitat Use and Water Temperature | 39 |
| 3.3.2. Turtle Captures and Decoys | 43 |
| 3.4 DISCUSSION | 43 |
| 3.4.1. Upper Murray River Distribution | 43 |
| 3.4.2. Capture Methods | 46 |
| 3.4.2. Conclusion | 48 |
| CHAPTER 4: GROWTH AND REPRODUCTION | 49 |
| 4.1 INTRODUCTION | 49 |
| 4.2 MATERIALS AND METHODS | 52 |
| 4.2.1. Data Collection | 52 |
| 4.2.2. Reproduction | 55 |
| 4.3 RESULTS | 57 |
| 4.3.1. Growth and Maturity | 57 |
| 4.3.2. Reproduction | 63 |
| 4.4 DISCUSSION | 66 |
| 4.4.1. Growth | 66 |
| 4.4.2. Maturity | 70 |
| 4.4.3. Conclusion | 78 |

| CHAPTER 5: I | Fox R emoval | 80 |
|-------------------|---|-----|
| 5.1 INTR | ODUCTION | 80 |
| 5.2 MATH | ERIALS AND METHODS | 81 |
| 5.2. | .1. Study Sites and Experimental Design | 81 |
| 5.2 | .2. Fox Abundance | 82 |
| 5.2 | .3. Fox Removal | 87 |
| 5.2 | .4. Monitoring Fox Populations | 87 |
| 5.3 RESU | LTS | 88 |
| 5.3 | .1. Fox Abundance: Non-Removal Sites | 88 |
| 5.3. | .2. Fox Abundance: Removal Sites | 89 |
| 5.4 DISCU | USSION | 91 |
| Chapter 6: I A | IMPACT OF FOXES AND POPULATION MODE | L |
| 6.1 INTR | ODUCTION | 95 |
| 6.2 MATH | ERIALS AND METHODS | 97 |
| 6.2 | .1. Turtle Density, Size Structure and Survival | 97 |
| 6.2 | .2. Impact of Foxes | 99 |
| 6.2. | .3. Model Development | 100 |
| 6.2. | .4. Model Analysis | 101 |
| 6.3 RESU | LTS | 103 |
| 6.3 | .1. Densities, Survival and Size Structure | 103 |
| 6.3 | .2. Effect of Removing Foxes | 107 |
| 6.3 | .3. Population Growth and Fox Removal | 110 |
| 6.3 | .4. Model Results and Elasticity Analysis | 112 |
| 6.4 DISCU | USSION | 114 |
| 6.4 | .1. Catchability | 114 |
| 6.4 | .2. Survivorship and Population Growth | 116 |
| 6.4 | .3. Population Stability and Management | 123 |

| Chapter 7: Nesting Ecology | 126 |
|---|-----|
| 7.1 INTRODUCTION | 126 |
| 7.2 MATERIALS AND METHODS | 130 |
| 7.2.1. Nesting Habitat | 130 |
| 7.2.2. Predator Detection of Nests | 131 |
| 7.2.3. Nesting Behaviour and Predation Risk | 132 |
| 7.2.4. Detection of Predators | 132 |
| 7.3 RESULTS | 133 |
| 7.3.1. Nesting Behaviour | 133 |
| 7.3.2. Nest Habitat | 134 |
| 7.3.3. Predator Detection of Nests | 137 |
| 7.3.4. Predation Risk and Changes in Nesting Behaviour | 138 |
| 7.3.5. Detection of Predators | 140 |
| 7.4 DISCUSSION | 141 |
| CHAPTER 8: INCUBATION AND SYNCHRONOUS HATCHING | 149 |
| 8.1 INTRODUCTION | 149 |
| 8.2 MATERIALS AND METHODS | 151 |
| 8.2.1. Developmental Temperature and Hatching Synchrony | 151 |
| 8.2.2. Group Size, Nest Emergence and Predation Risk | 157 |
| 8.3 RESULTS | 157 |
| 8.3.1. Hatching Synchrony and Developmental Temperature | 157 |
| 8.3.2. Group Size, Nest Emergence and Predation Risk | 159 |
| 8.4. DISCUSSION | 160 |
| CHAPTER 9: GENERAL DISCUSSION | 167 |
| 9.1 KEY FINDINGS | 167 |
| 9.2 LIFE HISTORY AND PREDATION | 169 |
| 9.3 MANAGEMENT STRATEGIES | 172 |
| REFERENCES | 178 |
| APPENDIX | 210 |

Chapter 1 General Introduction

This thesis investigates the population and nesting ecology of the Murray River short-necked turtle (*Emydura macquarii*). It also assesses the impact of the introduced red fox (*Vulpes vulpes*) and evaluates direct and sub-lethal impacts of predation on reproductive success and the stability and growth of these turtle populations. Although foxes have been implicated in the decline or extinction of 30-50 Australian native mammals (Saunders *et al.* 1995), their impacts on reptiles have not been assessed.

The thesis is divided into three main sections; the first section (chapters 3 and 4) investigates the population ecology of *E. macquarii*, particularly evaluating habitat preferences, modification of capture techniques, growth and reproduction. Age and size at maturity can influence reproductive traits such as clutch size, frequency and annual variation, which in turn are important parameters for evaluating population dynamics. The relationship between growth and reproductive parameters of freshwater turtles is well understood in many North American turtles (e.g. Wilbur 1975, Galbraith and Brooks 1987, Rosen 1987, Mitchell 1988, Frazer *et al.* 1990b, Iverson 1991a), but there have been few long-term studies on Australian species (Parmenter 1976, Chessman 1978, Georges 1982).

The second section (chapters 5 and 6) describes a fox removal experiment designed to measure the effects of foxes on the population dynamics of *E. macquarii*, particularly survival and juvenile recruitment rates of turtles. Demographic models, commonly used to evaluate population stability of marine turtles (Crouse *et al.* 1987, Crowder *et al.* 1994, Heppell *et al.* 1996b), were used to assess whether Murray River turtle populations are declining at current predation rates and the effectiveness of possible management options.

The third section (chapters 7 and 8) describes the nesting biology of *E. macquarii* and includes analyses of nesting behaviour in relation to predation risk, as well as mechanisms or cues that foxes use to detect turtle nests. Synchronous hatching occurs with many precocial avian eggs, but has not been demonstrated in reptilian eggs. In turtle nests, where development is dependent on the position of the egg within the nest (Thompson 1983a), eggs that hatch synchronously could benefit by 'diluting' predation risk and emerging from the nest as a group. The presence and advantages of synchronous hatching in eggs of *E. macquarii* were investigated.

1.1 Murray River Turtles

Three species of freshwater turtle inhabit the Murray-Darling system in southeastern Australia (Cann 1998). All three species are pleurodiran (suborder: Pleurodira) and belong to the Chelidae, which are the dominant freshwater chelonian family in Australia. The family consists of aquatic or semi-aquatic turtles with species represented in New Guinea and South America (Cogger 2000). Two species of *Chelodina* and one species of *Emydura* inhabit the Murray-Darling system.

Chelodina longicollis, the eastern longneck turtle, is the most widely distributed turtle species throughout Australia. It inhabits most coastal and inland waterways throughout eastern continental Australia, from eastern South Australia to eastern Queensland (Cogger 2000). *Chelodina longicollis* is highly mobile, and is often found on land or in ephemeral swamps (Cann 1998). It is carnivorous, preferring fish, crustaceans and insects (Parmenter 1976, Georges *et al.* 1986). In localised areas, *C. longcollis* can reach densities of over 1000 turtles.ha⁻¹ (Parmenter 1976) and it is also very abundant on the Murray, where it exploits the temporary waters associated with the floodplain, as well as the mainstream and ox-bow lagoons (Chessman 1988b). Females grow larger than males and mature in 10-11 years, whereas males mature in seven years (Parmenter 1985). Oviposition occurs in spring (Goode 1967, Parmenter 1985) and females generally produce one clutch of 6-23 eggs per year (Parmenter 1976).

Chelodina expansa, the broad shell turtle, is the largest chelid turtle in Australia (Cann 1998), attaining a mass of over 5 kg and a carapace length of 500 mm (Goode 1967). In the Murray-Darling catchment, it is restricted to the

permanent water of the system (Cann 1998) and is rarely seen on land or basking. Oviposition predominantly occurs in autumn (Cann 1998), unlike the other two species that oviposit in spring, yet a small proportion of larger *C. expansa* are gravid in spring (Spencer unpubl. data, Judge pers. com.). *Chelodina expansa* produces 5-25 (Goode and Russell 1968) large (17g) eggs (Legler 1985) per clutch each year. *Chelodina expansa* is carnivorous, using its long neck to strike at unsuspecting prey, such as large fish and crustaceans, but will consume carrion (Cann 1998). It is considered rare, but this may only reflect its secretive nature and its totally aquatic habits (Thompson 1993). *Chelodina expansa* is believed to have inhabited the Murray system much later than the other two species, extending its range from Queensland (Cann 1998).

1.1.1 **Emydura macquarii**: The Murray Short-Neck Turtle

Emydura macquarii is currently recognised as a widespread species inhabiting the Murray-Darling drainage system, west of the Great Dividing Range, and with several forms distributed throughout eastern flowing rivers of coastal NSW and Qld (Cann 1998). *Emydura macquarii* is a medium sized turtle, compared to *Chelodina longicollis* and *Chelodina expansa*, growing to a carapace length of over 300 mm (Chessman 1978). In the Murray-Darling system, they are primarily confined to the permanent waters. They are omnivorous, consuming mainly filamentous algae, fish (usually the remains of European carp (*Cyprinus carpio*)) and insects (Spencer *et al.* 1998). Mating occurs from March to April (Cann 1998) and turtles over-winter in the water (Tasker 1991). Nesting occurs between late October and mid-December, and females generally produce 15-25 eggs per clutch (Chessman 1978). Females emerge from the water at dusk or before dawn to construct nests 1-200 m from water, often taking two hours to complete the nesting process (Spencer unpubl. data). Incubation takes over 70 days (Thompson 1983a) and hatchlings usually emerge from the nest at dusk, although they can emerge at other times of the day (Spencer unpubl. data.).

Emydura macquarii is sexually dimorphic, with females (carapace length >300 mm) growing much larger than males (carapace length 270 mm) (Chessman 1978). Adult male turtles are easily identified by the length of their tail (Chessman 1978). The position of the cloaca of sexually mature males is well past the posterior of the carapace when extended and females have a much smaller tail (Fig. 1.1).



Tails of male turtles are thick and long.

Tails of female turtles are small and 'short'.

Fig. 1.1. Differences in tail length between adult male and female *E. macquarii.* The tail of male turtles is much larger and longer than females.

1.2 The Red Fox in Australia and the Introduction of Generalist Vertebrate Predators

Predation on turtle nests is common in most populations. Raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*) are the major predators of most North American turtle nests (e.g. Cagle 1950, Wilbur 1975, Christiansen and Gallaway 1984, Iverson 1991a, Jackson and Walker 1997) but these are endemic and presumably the turtles have co-evolved with their predators (Thompson 1983b). The red fox (*Vulpes vulpes*) was introduced to Australia for hunting in the 1870s (Saunders *et al.* 1995) and rapidly dispersed across the continent following the spread of the rabbit (Williams *et al.* 1995). Foxes are present in all habitats throughout Australia, except the tropical north, and are considered Australia's second worst vertebrate pest species, after the rabbit (CSIRO, 1996). Predation on turtle nests by foxes was first reported by Parmenter (1976) and Green (1980), but Thompson (1983b) observed that 95% of turtle nests on the Murray River are destroyed annually, with foxes accounting for all but 2% of these nests.

The impact of foxes on Australian native fauna is restricted mainly to mammals and birds. There have been more than 25 studies on the diet of foxes in Australia (Saunders *et al.* 1995), and while they consume a range of vertebrate and invertebrate prey, rabbits and small to medium sized native mammals are clearly the preferred items (Newsome *et al.* 1996, Banks 1997). Because foxes are not native to Australia, popular media have extrapolated these dietary studies to infer that foxes have caused extinctions to native species and pose considerable threat to many more (Banks 1997). However, there are few data to either support or dismiss these claims, although the combination of foxes and rabbits is believed to have been particularly damaging to medium sized native mammals (1 kg-5.5kg)(Banks 1997). There is no response in the numbers of rodents to fox reduction, but predation on small kangaroos falls considerably (Banks 1997). Similarly, there have been reports of increases in the number of wallabies (*Petrogale lateralis*- Kinnear *et al.* 1998), numbats (*Myrmecobius fasciatus*- Friend 1990) and mallee fowl (*Lepioa oscellata* - Pridell and Wheeler 1990) following fox baiting. Many endangered mammals once common across Australia are now restricted to islands without foxes or small pockets on the mainland where foxes are uncommon.

The impact of foxes on reptilian communities is largely unknown and confined to dietary studies of foxes. Although reptiles are supplementary prey of foxes (Catling 1988), if predation levels on eggs are high enough to reduce juvenile recruitment, turtle populations may be at risk. Because foxes are not native to Australia, predation pressures are potentially additive, with most freshwater turtle populations evolving with some degree of nest predation (Thompson 1983b). The extent of predation pressures from native predators is unknown. Aboriginals consumed turtle eggs (Angas 1847) and dingoes (*Canis familiaris dingo*) and marsupial predators, such as the Tasmanian devil (*Sarcphilus harrisii*), quolls (*Dasyurus maculatus*, *D. geoffroyi* and *D. viverrinus*), and Thylacine (*Thylacinus cynocephalus*), were also possible consumers of eggs (Thompson 1983b). Land clearing has reduced the number and diversity of extant vertebrates species present on the Murray, but goannas, water rats and numerous bird species are all potential predators of nests. Whether foxes have just replaced past predators or added to predation on Murray River turtles is unknown, but the introduction of foreign vertebrate predators to an ecosystem can have deleterious effects on many native species (Fritts and Rodda 1998, Goldschmidt et al. 1993).

One such introduction has occurred on the island of Guam. The accidental introduction of the brown tree snake (*Boiga irregularis*) on Guam around 1950 led to the extinction of all but three native vertebrate species on the island (Fritts and Rodda 1998). Guam is the largest island in Micronesia and lack of coevolution between this introduced predator and prey is partly blamed for the extinction of all forest birds and mammals. The presence of alternate introduced prey also facilitated the spread of the snake throughout the island, while it was driving the naive, native prey to extinction (Fritts and Rodda 1998). A similar large-scale reduction in vertebrate species occurred in Lake Victoria in Africa in the 1980s when a large increase in numbers of the introduced Nile perch (*Lates* sp.) coincided with the reduction of almost 200 vertebrate species in Lake Victoria in less than a decade is possibly the largest

extirpation of vertebrates of last century (Goldschmidt *et al.* 1993). The disappearance of phytoplanktivore and detritivore cichlids has resulted in large algal blooms and an increase in atyid prawns, which have replaced the detritivorous haplochromines and altered the food web (Goldscmidt *et al.* 1993).

1.3 The Role of *E. macquarii* in the Murray River

Emydura macquarii could also fill a similar role in the Murray-Darling drainage system to the now extinct phytoplanktivore and detritivore cichlids in Lake Victoria in Africa. The River Murray is part of Australia's largest river system (Pressey 1990) and supplies the city of Adelaide the majority of its drinking water (Eastburn 1990). The Murray-Darling River system has immense economic and cultural value and supports the richest agricultural industry in Australia (Eastburn 1990). The flow of the Murray River is now regulated by of over 90 impoundments throughout its length, with the Hume weir, in the upper Murray, the largest (Jacobs 1990). Although the ecology of the River system is extremely complex, a consequence of the impoundments is the favouring of lacustrine over riverine species (Thompson 1993). Some species are significant simply because of their enormous biomass and energy consumption (Thompson 1993). Invertebrates are the major herbivores in the system, although some birds may also be important, and the major predators include invertebrates and fish (Boon *et al.* 1990). Turtles are among these

quantitatively important species. Up to 100 000 tonnes of freshwater turtle may inhabit the Murray River system (Thompson 1993) but their role in the ecosystem is unlikely to be confined to sheer numbers alone. *Emydura macquarii* is a major consumer of filamentous algae, with their diet consisting of more than 60% of various types of algae (Spencer *et al.* 1998). The turtle is also a major scavenger, with a large proportion of its diet consisting of carrion, predominantly the remains of the introduced European carp (Spencer *et al.* 1998). Thompson (1993) estimated that 180 000 tonnes of carrion could be consumed each year in the Murray River system by freshwater turtles, which is over 430 tonnes per day. The question is, if turtle populations are declining because of predation on nests by foxes along the Murray River, what would be the ecological consequences to the River system? The answer to that is not known, but there is potential for problems of eutrophication and changes in the ecological structure of the River system analogous to that in Lake Victoria.

1.4 Evaluating Population Declines

We do not know the longevity of turtles in the Murray River, but like many freshwater turtles (Gibbons and Semlitsch 1982), they are probably long lived. *Chelodina longicollis* matures as late as 10 years, lives in captivity for up to 36 years (Goode 1967) and potentially as long as 150 years in the wild (Parmenter 1985). Some adult turtles alive today were potentially present before foxes were introduced to Australia in 1870, and a lack of juvenile recruitment from fox predation will take a long time to become evident as a sharp decline in population numbers (Thompson 1993). The majority of turtles in the Lake Bonney (South Australia) population of *E. macquarii* consist of large older individuals and nest predation rates are over 95%. Foxes on the Murray have caused a lack of juvenile recruitment and a 'top heavy' size structure compared to the population in the Cooper Creek, where foxes are rare, are more evenly distributed (Thompson 1983b).

Using size distributions of a population as evidence of possible declines may be inaccurate, particularly with turtles, unless reasonable estimates of survival, growth and fecundity are available, because parameters such as age at maturity, clutch size and frequency, can vary significantly between species and among populations of the same species (see Shine and Iverson 1995). Survival rates of the different life stages of turtles are particularly important for estimating population declines (Gibbons 1987). In general, most living populations of animals can be described by one of three types of survivorship curve (Krebs 1994), with survivorship of different turtle populations falling into one of two of these categories (Wilbur 1975, Iverson 1991b).

Most animals with a Type I survivorship curve will die in the postreproductive stage (Fig. 1.2) i.e. at the end of a physiological life span. Only humans and large mammals in favourable conditions exhibit this type of survivorship (Krebs 1994).



Fig. 1.2. Survivorship curves. Type I curve: most mortality occurs in the postreproductive stage. Type II curve: mortality is constant throughout each life stage. Type III curve: most mortality occurs in the pre-reproductive stage.

Freshwater turtles have been described as having a Type II survivorship curve (Wilbur 1975, Tinkle *et al.* 1981, Mitchell 1988) where mortality is relatively constant throughout the life stages (Fig. 1.2). In species exhibiting this sort of survivorship pattern, size distributions are relatively evenly spread with juvenile and adult turtles (Wilbur 1975, Mitchell 1988). However, the pattern of survivorship of freshwater turtles is best described by a Type III curve, where survivorship is related to age (Iverson 1991b) i.e. mortality greatest in the egg, hatchling and juvenile stages. Often survival of the adult stage exceeds 90% (see Shine and Iverson 1995) in freshwater turtles and the size distributions of species with Type III survivorship patterns will mainly consist of adults, as juvenile recruitment is low.

Turtles occur in large numbers on the Murray (Chessman 1978) and, along with their longevity, evaluating the impact of foxes is difficult. Life tables have been used to evaluate the survival, growth and fecundity schedules of turtles (Iverson 1991a), but require many years of study to observe population declines and are only useful when the majority of individuals can be aged. Demographic models are useful to evaluate population growth or declines of long-lived species (Heppell et al. 1996b, Crouse et al. 1987). They use current day values of survival, growth and fecundity to predict population stability and extinction rates. Demographic models have been used to estimate declines in many marine turtle populations and evaluate the success of current management strategies (e.g. Crouse et al. 1987, Crowder et al. 1995, Heppell et al. 1996a). Most conservation efforts focus on headstarting programs (Crouse et al. 1987), which have had little or no effect on reversing marine turtle declines. Only recently have management strategies directed effort to reducing the mortality rates of adult and large juvenile turtles, which are far more critical to population stability than earlier stages (Crouse et al. 1987).

1.5 Aims and Scope of this Thesis

After Thompson (1983b) reported extremely high nest predation rates on the lower Murray, there has been only one study that looked at aspects of the population dynamics of Murray River turtles (Spencer 1995). The upper Murray was chosen to determine whether fox predation on turtles and their nests is restricted only to the lower parts of the Murray (Thompson 1983b), or if it is a general occurrence that can apply to the whole Murray system. The impact of foxes on the population dynamics of *E. macquarii* is also determined by developing accurate estimates of growth, survival and fecundity, and using demographic models to test the null hypothesis that predation pressures by foxes are having no effect on the population growth or stability of populations of *E. macquarii*.

Following a description of the study areas in Chapter 2, Chapter 3 determines the main habitat utilised by *E. macquarii* in the upper Murray, as well as development of capture techniques to maximise catch rate. Growth rates of *E. macquarii* are determined in Chapter 4, which includes an evaluation of growth annuli and common growth models as methods to age *E. macquarii*. The reproductive strategy, such as relationships between body size and reproductive parameters, especially clutch frequency and sizes are also determined. Annual clutch size variation and its relationship to possible environmental conditions are also evaluated. A fox removal experiment (Chapter 5) was used to determine whether predation has an impact on the population dynamics of *E. macquarii* (Chapter 6). Chapter 6 also assesses the future success of possible management options. In Chapter 7, I determine the impact of predation risk of reproductive success and nesting behaviour, as well as mechanisms by which foxes detect turtle nests and the habitats where predators are least likely to discover nests. Chapter 8 concentrates on the hatching synchrony in eggs of *E. macquarii* and the mechanisms by which it may occur, as well as the selective advantages and disadvantages in hatching synchronously. The last chapter presents a synthesis of the results and considers the implications of fox predation on the other Murray River turtle species, and to the management of foxes in Australia.

Chapter 2 Study Sites and Methods

2.1 Study Sites

2.1.1 Location

The River Murray can be divided into five distinct regions (Mackay 1990).

1. **The headwaters** run from the source in the Snowy Mountains to Corowa and consist of about 450 river km.

2. **The riverine plains** are vast flat tracts where the River flows 800 river km in shallow channels from Corowa to the Wakool Junction.

3. **The Mallee trench** extends from 850 river km down to Overland corner.

4. **The Mallee gorge:** the River has cut through hard limestone rock during a period of low sea level, forming steep cliffs. Salty ground water enters the River through aquifers in the cliff face in the gorge.

5. **The Lakes and Coorong**. Lake Alexandrina and Albert, together with Coorong, once formed a huge estuarine system, but barrages now separate the Lakes from the Coorong and retain freshwater.

My study sites were located in the upper Murray River, in the Albury region (187m above sea level) below Lake Hume, and in the Lake Mulwala region (Fig. 2.1). Thus the sites include the lower part of the Murray headwaters, as well as the riverine plains. Four lagoons were selected to evaluate the impact of foxes and the population dynamics of *E. macquarii*. Hawksview and Snowdon's lagoons are located east of Albury below Lake Hume in New South Wales and Victoria respectively, whereas Cook's and Bankview lagoons are west of Albury (Fig. 2.1). Hawksview and Snowdon's lagoon are located 12 km from Albury and are relatively close to each other (<2 km) but separated by the River (Fig. 2.1). Cook's lagoon is 4 km from Albury and Bankview lagoon is 12 km further west of Cook's, less than 10 km from Howlong township.



Fig. 2.1. Location of study sites on the Murray River. The highlighted regions shows the location of Victoria in Australia and the location of study sites on the New South Wales and Victoria border respectively. Location of the main study lagoons in the Albury-Wodonga region shown by coloured markers in the top figure.

Cook's

• Bankview

Snowdon's

Hawksview

2.1.2 Vegetation

Much of the land between Hume weir and Lake Mulwala has been subject to large-scale vegetation clearing since settlement (Smith and Smith 1990) and is now mainly grassy plain (Fig 2.2). Introduced weeds constitute a third of all plant species and the main weed families are the grasses and daisies. The bromes (*Bromus* spp.), barley grasses (*Hordeum* spp.), ryegrasses (*Lolium* spp.), sow-thistles (*Sonchus* spp.), Narrow-leaved clover (*Trifolium angustifolium*) and Paterson's Curse (*Echium plantagineum*) are common weeds in the area. Tussock grass (*Poa labillardieri*), Moira grass (*Pseudraphis spinescens*), Mat grass (*Hemicarthria uncinata*), common sneeze weed (*Centipeda cunninghami*), black rush (*Juncus amabilis*) and soft sedge (*Carex gaudichaudiana*) are common native vegetation. River red gums (*Eucalyptus camuldensis*) and silver wattle (*Acacia dealbata*) are relatively common native trees and introduced weeping willows (*Salix babylonica*) dominate patches of the banks of the lagoons, lakes and river.

2.1.3 Climate

The lagoons are located 170 m above sea level at the base of the Snowy Mountains (Fig. 2.2). Winters are relatively cold, with mean maximum and minimum temperatures of 12.5 °C and 2.8 °C in July. Morning frosts are common from mid March through to October and summer is characterised by relatively hot days (mean max. 30.1 °C in January and February) and mild nights (mean min. 14.7 °C in January). Mean daily temperatures increase rapidly in spring from September (16.9 °C) to October (20.6 °C) and November (28.0 °C), with similar proportional increases in mean minimum temperatures for the same period (Bureau of Meteorology unpubl. data).



Fig. 2.2. The upper Murray River. The River initially flows into Lake Hume. Water flow is regulated from Lake Hume and the River flows through relatively flat open pastures used for cattle and sheep farming. Lake Mulwala is the next major impoundment downstream of Hume weir. Copyright 1996 & 1999 -(<u>kathyw@albury.net.au</u>) Reproduced with permission. Typically, rainfall is more seasonal in the Albury district than at Corowa (Lake Mulwala), with winter much wetter than summer (Fig. 2.3). Corowa experiences similar summer rainfall to Albury, although much less rain falls in winter. On average 754.2 mm and 542.3 mm falls at Albury and Corowa respectively (Bureau of Meteorology unpubl. data). High rainfall in the winter and spring of 1996 resulted in flooding in the Albury area, connecting Cook's lagoon to the mainstream and filling the other lagoons. Annual rainfall for 1996 and 1998 was close to the average at both areas, but total rainfall in 1997 (and beginning of 1998) was well below average with both areas received almost half that of the previous year (Fig. 2.4). At the beginning of 1998, Albury and Corowa were declared drought regions, primarily due to the low winter and spring rainfall in 1997 and high daily temperatures over summer. Corowa and Albury had record low rainfall for the first two months of summer during this period (Fig. 2.3).

2.1.4 Lagoon habitat

The water quality varies significantly among lagoons because of local differences in groundwater, soils, vegetation and wind action (Boon *et al.* 1990). The water in all the lagoons is extremely turbid and in both Snowdon's and Hawksview lagoons, blue-green algae blooms (*Anabaena* spp.) are common in summer. Thick, bright green clumps of blue-green algae are usually located on the surface of the water close to the shoreline. Water temperatures in each lagoon ranged from below 8 °C (7.3 °C July 1996) to above 30 °C (33.4 °C February 1998).

(a) Albury Airport





Fig 2.3. Monthly rainfall (mm) for (a) Albury Airport (Albury area) and (b) Corowa Airport (Lake Mulwala area) (solid bars) during 1996-1999, with mean monthly rainfall (trend line) for the region (Bureau of Meteorology unpubl. data).



Fig. 2.4. Rainfall (mm) differentials from mean rainfall per month at (a) Albury airport (Albury area) and (b) Corowa airport (Lake Mulwala area) (Bureau of Meteorology unpubl. data).

Soil type also varies considerably among lagoons: Hawksview consists of a sand base with large amounts of sediment in some areas; Bankview has a light clay based soil and both Cook's and Snowdon's lagoons have thick, mud sediment base. There is virtually no aquatic vegetation present in the lagoons, with only Bullrush (Typha spp.) visible, but numerous algae (phytoplankton and filamentous) occur at all times of the year. European carp (Cyprinus *carpio*) are common in all aquatic habitats, and red-fin (*Perca fluviatilis*), yellowbelly (Macquaria ambigua) and yabbies (Cherax destructor) are also common. Magpies (Gymnorhina tibicen) and noisy miners (Manorina *melanocephala*) are common around all study sites, and several birds of prev (wedge-tailed eagles (Manorina melanocephala), and whistling kites (Haliastur *sphenurus*)) also occur there. Purple swamp hens (*Porphyrio porphyrio*) are found around the banks of the lagoon, near the cover of willows and Bullrush (*Typha* sp.). Semi-aquatic birds such as the black swan (*Cygnus atratus*), pelicans (*Pelecanus conspicillatus*) and numerous duck species are abundant at various times of the year at most sites. The most common snake found is the red bellied black snake (Pseudechis porphyriacus), but brown snakes (Pseudonaja textilis) and tiger snakes (Notechis scutatus) are not uncommon. Agricultural livestock are the predominant mammal species around the study sites but rabbits (Oryctolagus cuniculus), hares (Lepus capensis) and brush-tail possums (Trichosurus vulpecula) are common.
2.1.5 Hawksview

Hawksview lagoon is less than 1 km from Lake Hume on the New South Wales (northern) side of the Murray River (Fig. 2.5). The lagoon is divided by a dirt causeway to allow easy transfer of cattle and essentially two separate lagoons exist, only connected by a small concrete pipe with wire mesh at each end to allow water transfer. The two lagoons were connected during the floods in August 1996, although Hawksview was not connected to the mainstream during this period. The northern lagoon is much smaller than the lagoon south of the causeway and the mark-recapture study of *E. macquarii* was conducted in this smaller lagoon. The width of each lagoon is similar along its length and the banks between and around each lagoon are relatively steep, with 1-2 m between the water and top of the bank on both sides. There are a few low level points along the length of the banks, particularly at the southern end of the larger lagoon and the northern end of the smaller lagoon. The lagoons are at the base of a valley, with land to the west being very flat and to the east rising steadily to a series of hills that surrounds Lake Hume. The base of the lagoon is sandy with a large build up of silt in most areas, creating thick layers of mud. No truly aquatic vegetation were found in the lagoon, however Bullrush (Typha sp.) and Phragmites australis are scattered throughout the shallower regions. Willows (*Salix* sp.) are scattered along the lagoon and their branches protrude almost 10m over the water surface. River Red Gums (Eucalyptus camaldulensis) are scattered throughout Hawksview, but the surrounding land is predominantly cleared for cattle and sheep

grazing. The land at the northern end of the smaller lagoon is low and the majority of turtles from this lagoon emerge and nest there. Turtles in the larger, southern lagoon mainly emerge and nest to the south. With the majority of nesting occurring at separate ends of each lagoon, the turtle populations are likely to be distinct populations. The total length of the lagoon is 2.25 km but the smaller lagoon used for the mark-recapture study is 0.8 km. This smaller lagoon (now referred to as Hawksview lagoon) was more manageable and used to evaluate growth (chapter 4) and population dynamics (chapter 6) of *E. macquarii* and was a fox removal site (chapter 5).



Fig. 2.5. Topographic map (Vicmaps-1:25 0000) and photo of Hawksview lagoon.

2.1.6 Bankview

Bankview lagoon is west of Albury, on the NSW side of the River (Fig. 2.6). The lagoon is less than 1 km from the mainstream, but is rarely connected to the River including during the floods in 1996. The lagoon has a light clay base and numerous submerged logs. Red Gums are present around the lagoon and the surrounding land has been cleared for cattle grazing and pastures. Willow's are distributed in patches along the banks of the lagoon and there are no submerged macrophytes present. The area is extremely flat and to the west of the lagoon is a gravel pit. Water level varies seasonally, but the lagoon is at least 2 m deep in January (summer) and only a small area of the southern end of the lagoon becomes dry. The lagoon is 1 km long and between 50 m and 100 m wide. This lagoon was used to evaluate growth (chapter 4) and population dynamics (chapter 6) of *E. macquarii* and was a fox control (non-removal) site (chapter 5).





Fig. 2.6. Topographic map (Vicmaps-1:50 0000) and photo of Bankview lagoon

2.1.7 Snowdon's

Snowdon's lagoon is situated on the Victorian side of the River and is less than 1 km from the mainstream (Fig. 2.7). The western half of the lagoon regularly dries during summer but the bay on the eastern half of the lagoon is very deep (>3m). Large sediment deposits have created a thick mud base of the lagoon and no submerged macrophytes are present, but Bullrush (*Typha* sp.) is common. The surrounding banks have been cleared for cattle grazing and are easily accessed by nesting turtles, but willows and red gums are present. The lagoon is 3.1 km long and was used to evaluate growth (chapter 4), population dynamics (chapter 6) of *E. macquarii* and was a fox removal site (chapter 5).



Fig. 2.7. Topographic map (Vicmaps-1:25 0000) and photo of Snowdon's lagoon

2.1.8 Cook's

Cook's lagoon is located west of Albury on the NSW side of the River and Albury City council owns the surrounding land (Fig. 2.8). In 1996 and 1997 the area was used for cattle grazing but a hardwood plantation was planted on the western side of the lagoon during 1998 and several levy banks and ponds were created close to the highway. The surrounding land and the lagoon were connected to the mainstream by the floods in 1996 and small creeks from the lagoon to the River were often full during periods of high rainfall. This lagoon was used as a fox control (non-removal) site but not used to evaluate growth and population dynamics of *E. macquarii*.



36004'00"



Fig. 2.8. 1:50 0000 topographic map (Vicmaps) and photo of Cook's lagoon

2.1.9 Mulwala Lagoon

The lagoon is on the northern side of Lake Mulwala (36° 00' 45"E 146° 10' 00"S-Fig. 2.1) and is a backwater of the Lake (Fig. 2.9). Turtles often bask on the numerous fallen logs and drowned trees present in the lagoon. Large clumps of aquatic macrophytes (*Valisnaeria giganteous*) occur in patches of the lagoon and the water level remained relatively constant throughout the study period because it is controlled by water release from Mulwala weir. The lagoon is surrounded by River red gum and pelicans, swans and various species of duck are common throughout the year. The lagoon is circular and relatively small (<500 m diameter). Mulwala lagoon was used to evaluate reproductive parameters of *E. macquarii* (Chapter 4) and for collection of eggs for hatchling release (Chapter 4) and the hatchling synchrony experiment (Chapter 8).



Fig. 2.9. Mulwala lagoon

2.1.10 Lake Mulwala

Lake Mulwala was created when the River was impounded between Yarrawonga and Mulwala, resulting in a 6000 ha lake. Many dead trees are present in the lagoon (Fig. 2.10), standing on land that was used for agricultural before the creation of Yarrawonga weir. Over 20 islands are present at the eastern end of the Lake where the Ovens River joins the Murray. Some of these islands cover more than 10 ha and were believed to be important recruitment areas for juvenile turtles, because they may provide some relief from fox predation (Thompson 1993). However, searches revealed that foxes use and swim between islands. Much of my work was conducted in a small bay approximately 5 km downstream of Mulwala lagoon on the NSW side of the Lake (36° 00' 15"E 146° 04' 00"S) where I captured the majority of turtles for egg collection (Chapter 8) and reproductive condition (Chapter 4). The area is relatively shallow (<2 m) and the Lake bed is compacted fine sand (silica). No macrophytes are present in the bay but large patches of *Valisnaeria giganteous* are present elsewhere throughout the Lake. The bay has numerous partially submerged logs and turtles were observed basking throughout the day.





Fig. 2.10. Lake Mulwala. Small islands are visible in the second photo.

2.2 Turtle Capture

2.2.1 Hoop traps and other capture methods

Turtles of the genera *Trachemys* (Tucker and Moll 1997), *Chelydra* (Tucker 1994), *Kinosternum* (Iverson 1989) and the Australian turtles *Emydura* (Chessman 1986) and *Chelodina* (Kennett and Georges 1990) are commonly captured in baited hoop traps (Legler 1960a). *Emydura macquarii* were predominantly captured in hoop traps with a trap entrance in an inward rectangular funnel (300 mm wide and 120 mm deep). Traps were baited predominantly with ox liver and placed into bait cages in the centre of the trap (chapter 3).



Fig. 2.11. Hoop trap with bait cage located in the middle of the trap. Two *E. macquarii* are visible at the front of the trap.

Trapping occurred in 10-18 day intervals monthly within Hawksview, Bankview and Snowdon's lagoons between September and March of each year from 1996 to 1999. Six traps within each lagoon were stretched between two 1.5 m long wooden stakes in waist deep-water (1.2 m). The back ring of each trap was partially emerged to allow captured turtles within the traps to breathe (Fig. 2.12). Traps were set 10 m apart within each lagoon and were checked twice daily (08:00 and 18:00). Trapping occurred in Mulwala lagoon and Lake Mulwala in October and November each year. All captured turtles were removed and traps were reset with fresh bait.



Fig. 2.12. A hoop trap set in Hawksview lagoon. The back rings are set out of the water to allow turtles to breathe.

2.2.2 Captured turtles

Each captured turtle was sexed (Cann 1998) and weighed to the nearest 25 g using 10 kg spring balance. Smaller turtles (<500g) were weighed to the nearest 10 g using a 1 kg spring balance. Curved and straight carapace (CL)

and plastron (PL) lengths were measured to the nearest 1 mm with a tape measure and callipers. The vertical distance between the top of the carapace and the plastron was measured with callipers. Each turtle was furnished with a unique combination of notches in the marginal scutes and underlying bone (Thompson 1982) with an angle grinder (Ryobi 10mm) or bastard file. Marked turtles were released at their point of capture within 12 hours.

2.2.3 Egg collection, incubation and hatchlings

Female turtles were held vertically and palpated by placing both index and middle fingers between the left and right back leg pits to locate oviductal eggs. Gravid female turtles were given a subcutaneous intramuscular injection of 2 ml of oxytocin (Syntocin, Ilium[™]) in the thigh (Ewert and Legler 1978) and placed in enclosed cardboard containers. Most females began to oviposit within 30 min. Eggs were uniquely marked using a HB graphite pencil and placed into a mixture of two parts vermiculite to one part water by weight in foam containers (1000mm x 400 mm x 350mm). All eggs were transported to the University of Sydney within 24 hours of collection. Eggs were incubated in vermiculite approximating -370 kPa on the basis of similar vermiculite calibrated using thermocouple psychrometry and a Wescon C52 sample chamber connected to a Wescon KR33T micro voltmeter. Containers were monitored daily and any eggs that died throughout the incubation period were removed immediately and distilled water was used to compensate for small water losses from the incubation boxes. Hatchlings were

toe clipped with unique combinations that distinguished between clutch and temperature treatment only. Only one toe from each foot was clipped and no more than three feet were clipped on each individual. Hatchlings were weighed and their plastron and carapace lengths and widths measured before release.

Chapter 3 Distribution of Turtles and Development of Capture Techniques

3.1 Introduction

In Riverine systems there are three main habitats that freshwater turtles inhabit, the mainstream, lakes and lagoons. Mainstreams are usually allochthonous (ie. derive organic energy from outside the stream) and are dilute biological systems, whereas lagoons or billabongs are autochthonous and highly productive as they have a high biomass to water volume compared to the river and actually contribute organic matter to the system (Boon *et al.* 1990). Snapping turtles (*Chelydra serpentina serpentina*) occupy habitats with a range of productivities in Ontario, Canada. Within the warmer, productive areas turtles grow almost four times faster and produce clutches 30% larger than turtles in less productive areas (Brown *et al.* 1994). If the quantity or quality of food available to turtles is higher in more productive habitats, the thermal and spatial ecology of turtles will be affected, because the density and biomass of turtle increases with productivity (Congdon *et al.* 1986).

Freshwater turtles rival fish in terms of their biomass in the River Murray system, and the Murray Short-Necked turtle, *Emydura macquarii*, is probably its most abundant species of freshwater turtle (Thompson 1993). *Emydura*

macquarii has been caught mainly in the mainstream and backwaters (abandoned meanders still connected to the river) in the middle reaches of the River (Chessman 1988b), but the distribution of turtles near large dams could be considerably different. Summer mainstream water temperatures in the middle reaches the Murray River are close to 30° C, but Lake Hume is thermally stratified and the release of relatively cold water has reduced summer water temperatures by almost 6° C, with seasonal water temperature patterns delayed by one month (Shafron *et al.* 1990). At both dammed and undammed sites in North America, western pond turtles (*Clemmys mormarata*) inhabit deep water, but they are only associated with basking structures at dammed sites, which are important for thermoregulation because of the low water temperatures (Reese and Welsh 1998).

Emydura macquarii is omnivorous and scavenges predominantly on large dead fish such as the introduced European carp, *Cyprinus carpio* (Spencer *et al.* 1998). When food such as a large dead fish is located by *E. macquarii*, feeding can be violent with both the muscular jaw and large claws used to tear flesh from the carcass. Such food items are not common in the environment (Spencer *et al.* 1998) and the activity of a turtle feeding may attract other turtles that are searching for similar food. Similarly turtles feeding within traps should attract other turtles to the trap and thus increase the capture rate significantly.

The aim of this study was to maximise capture success in the upper Murray River by determining habitat use of *E. macquarii* and developing capture techniques using hoop traps. Habitat preference in relation to thermal regime and the effect on reproduction was also determined.

3.2 Materials and Methods

3.2.1 Habitat and Distribution

Hoop traps were set in the mainstream near Corowa NSW (n=4), in a lagoon associated with Lake Mulwala (Mulwala lagoon, n=4) and on the northern shore of Lake Mulwala (n=4). Traps were baited with ox liver and set in October 1996 for one week. The experiment was repeated in February 1997 when the ambient and water temperatures were warmer, however traps were placed in a lagoon near Albury (Bankview lagoon), the mainstream immediately below Lake Hume and the southern shores of Lake Hume (Fig. 1). Water temperatures (0.5 m deep) were recorded at 17:00 daily. Traps were checked twice daily at 08:00 and 17:00 and the numbers of captures were recorded at each trapping session. Turtles were measured, marked and released within 12 hours of capture (chapter 2). A one-way ANOVA with captures per trapping session was used to compare rate of capture of turtles between the mainstream, lagoon and Lake in October and repeated using the February data. Tukey HSD pairwise comparisons were used to determine significant differences in capture rate among sites.

3.2.2 Maximising Trap Success

To determine whether feeding turtles attract other individuals into traps, I used Bankview and Hawksview lagoons. Six traps within each lagoon were set (chapter 2) using ox livers in bait cages to attract *E. macquarii* to the traps. Bait cages, used to minimize consumption of the ox liver and increase the possibility of attracting more turtles into the trap, consist of a 200 mm pouch made from plastic garden lattice (mesh size 15mm x 10mm), with the bottom and sides held together with plastic cable ties. Once bait is placed into the cage and the hoop traps set, the cage is suspended mid-trap, and it is impossible for a turtle or fish to access the bait without entering the trap. The attractiveness of the bait to the turtle is not lost because the scent of the bait is not restricted and the turtle is able to take small bites of the bait, enticing it to remain in the trap and possibly attracting other turtles to feed within the trap. For the first trapping session, traps were set before 12:00 and checked at 15:00. Captured turtles were removed from traps and individually marked (chapter 2). Three marked turtles, or decoys, from each lagoon were placed in every second trap (one turtle per trap) at the end of each trapping session, and traps were checked at 06:00 and 18:00 daily for four days. Bait was replaced with fresh ox liver each session. Total number of new *E. macquarii* captured in each trap was recorded at the end of each session, and analysed using a t-test. In 1995 and 1996, a similar trapping regime occurred in the same lagoons without decoys present.

3.3 **Results**

3.3.1 Habitat Use and Water Temperature

Over the week in October, 68 turtles were captured in Mulwala lagoon, 43 in Lake Mulwala, and only five in the mainstream near Corowa. The capture rate in the lagoon was steady throughout the trapping period, but in Lake Mulwala the capture rate was erratic, with one trapping session yielded 21 animals whereas all other sessions yielded fewer than five turtles. Thus, there is a sharp increase in the curve of cumulative captures, followed by the curve levelling out (Fig 3.1a). October capture rates were analysed excluding the first two trapping sessions from each site. The large capture (21 turtles) during the second trapping session in Lake Mulwala was against the trend for the rest of the week (Fig 3.1a), so the data point was isolated and is discussed separately. Excluding the first two trapping sessions at each site in October yields similar trends to the Albury sites. The capture rate between sites was significantly different ($F_{2,33}=24.7$ p<0.001), with more turtles captured in the lagoon compared to the Lake (p<0.001) and the River (p<0.001), but there were no differences in the capture rate between the Lake and the mainstream (p=0.2).

Similarly there were differences in the capture rate between the Albury sites $(F_{2,39}=31.9 \text{ p}<0.001)$. Significantly more turtles were caught per trapping session in Bankview lagoon compared to both Lake Hume (p<0.001) and the

mainstream below Lake Hume (p<0.001), as well as between Lake Hume and the mainstream (p=0.02) (Fig. 3.1b). Trapping at the other different locations in both Lake Hume and Lake Mulwala yielded no turtles over the various time periods.

Water temperature of Mulwala lagoon varied between 21.8 °C and 24.3 °C over the week in October, whereas in February, Bankview lagoon was considerably warmer, varying between 27.3 °C and 28.5 °C. Lagoons were consistently warmer than lakes and lakes remained warmer than the mainstream (Fig 3.2). Although the water temperature of Lake Mulwala was initially warmer than the mainstream at Corowa, it dropped below that of the Lake on the third day of trapping (Fig 3.2a).



Fig 3.1 (a) Cumulation curve of turtle captures over a one-week period in Mulwala lagoon, Lake Mulwala and the mainstream near Corowa.(b) Cumulation curve of turtle captures over a one-week period in Bankview lagoon, Lake Hume and the mainstream below Lake Hume.



Fig 3.2(a) Water temperature of Mulwala Lagoon, Lake Mulwala and the River near to Corowa over a one week period in October 1996. **(b)** Water temperature of Bankview lagoon, Lake Hume and the River below Lake Hume over a one week period in February 1997.

3.3.2 Turtle Captures and Decoys

A total of 82 *Emydura macquarii* were captured, with only one recapture over the four-day period (not included in the analysis). Traps with decoy *E. macquarii* successfully captured both adult and juvenile turtles (57 adults [31 female and 26 male] and six juveniles). Baited traps also caught both adult and juvenile turtles (16 adults [10 female and 6 male] and three juveniles), but significantly fewer were captured compared to traps with the decoys ($t_{13} =$ 5.9, p<0.001). Over the same period, two *Chelodina longicollis* and three *C. expansa* were captured in traps without *E. macquarii* decoys present.

3.4 Discussion

3.4.1 Upper Murray River Distribution

Upper Murray River lagoons provide greater and more consistent capture rates than either Lakes or the mainstream. Chessman (1988b), however, captured the majority of *E. macquarii* in the mainstream and backwaters and proportionally fewer in lagoons and anabranches, at study sites including much of the middle region of the River. Water temperature may account for the difference in habitat preference of *E. macquarii* between this study and Chessman's (1988b). Water temperatures of the mainstream are relatively low in the upper Murray River because of the release of cool water from Lake Hume (Shafron *et al.* 1990), and *E. macquarii* may have 'shifted' habitat preference from the mainstream to the warmer lagoons in this area. Turtles inhabit the mainstream in the middle part of the River (below Lake Mulwala) because they are sufficiently warm to maintain metabolic processes (Chessman 1978).

With higher densities of turtles present within lagoons, compared to the lakes or the mainstream, increased trap success is possible because more turtles will pass by, and be attracted to, the trap over a period of time. Conversely, because the lagoon is more productive than the Lake and more food could be available elsewhere in the lagoon, capture rates were not as high as the second session in Lake Mulwala (Fig. 3.1a). In Lake Mulwala, large numbers of turtles may be attracted to the traps initially because the bait is a much richer source of food relative to that available in the Lake. The trapping location in Lake Mulwala may not be representative of many other parts of the Lake, which may imitate the low capture rate in Lake Hume. Trapping in other locations within both Lake Hume and Lake Mulwala failed to capture any turtles, suggesting that densities are not evenly distributed in Murray River lakes. High-density clusters of turtles are likely to be found where food and favourable thermal conditions exists in various parts of the Lake. These areas may be similar to the backwaters of the River i.e., still connected, but an abandoned area of the River's meander (Chessman 1988b), where the water can warm considerably due to low flow rate. The trapping area in Lake Mulwala was shallow enough to allow adult *E. macquarii* to bask on partially submerged logs (Chessman 1987) and was relatively enclosed and sheltered

from large external influences that act on the main Lake, such as cool southerly winds. Consequently, the water within the bay may be warmer and less turbulent than the majority of the Lake. However, despite the bay being relatively enclosed and protected, the water temperature in this area was more variable than either Mulwala lagoon or the mainstream (Fig 3.2a). A cold front and thunder storm passed through the Mulwala region after the second trapping session and water temperatures decreased by almost 4 °C in the Lake, compared to less than 1 °C decrease in both the lagoon and the River (Fig 3.2a). In fact, water temperature of the Lake nearly decreased to the minimum water temperature at which *E. macquarii* feeds (16.3 °C- Chessman 1988b). During this period, turtle capture rate decreased sharply and remained at zero captures for five trapping sessions.

Two major factors influencing the distribution of *E. macquarii* in the Murray River is food availability and thermal environment. *Emydura macquarii* feed predominantly on filamentous algae (Spencer *et al.* 1998) or aquatic macrophytes (Chessman 1986) and carrion (Chessman 1986, Spencer *et al.* 1998) that are all in large volumes within Murray lagoons. Very high clorophyll-a concentrations (reflects algal biomass) of up to 1500 μ g/L occur during late summer in lagoons near Albury compared to algal concentrations in the mainstream that rarely exceeds 10 μ g (chlorophyll-a).L⁻¹ (Boon *et al.* 1990). However, *E. macquarii* is unable to survive on a diet consisting only of aquatic macrophytes and must supplement its diet with carrion (Teleostomi), predominantly European Carp (*Cyprinus carpio*), and macro-invertebrates (Spencer *et al.* 1998). The macro-invertebrate communities of lagoons are taxonomically distinct from mainstream communities and their biomass is much higher (Boon *et al.* 1990). Similarly European Carp (*Cyprinus carpio*) are present in large numbers in each lagoon (personal observation).

The body temperature of ectotherms is determined primarily by passive heat exchange with its environment (Withers 1992). Both lagoons were consistently warmer than the Lakes and the mainstream (Fig. 3.2) in spring and summer. Turtles with higher body temperatures can consume and assimilate more food and energy than cooler turtles (Spencer *et al.* 1998), and being ectothermic, they need to gather it over a long period prior to the time of ovulation (Fraser 1980, Reznick 1983). This may have important implications for the timing of nesting and incubation conditions of the nest. In hot and dry conditions, *E. macquarii* may reduce clutch size to avoid desiccating incubation conditions (chapter 4) and individuals that produce clutches early may avoid these conditions and potentially increase clutch success.

3.4.2 Capture Methods

The presence of a turtle within a trap also attracts other turtles to that trap, probably because of the activity and movement caused by feeding. Once a few turtles (~3 turtles) have entered the trap, the combined activity of the turtles feeding may lead to a 'feeding frenzy', as the attraction to the trap may

increase as each turtle enters. Ten turtles were caught in one trap during the third trapping session and it was common to have six or seven in a trap. The length of a trapping session may also be important for capture success. If traps are checked too regularly (i.e., within 2 hours), there is a strong possibility that turtles will be scared away from the area and the capture rate will be reduced. However, if traps are checked infrequently, bait will be consumed or become rotten and trap success will also be reduced. The trapping period for this study was twelve hours, possibly long enough to attract turtles to the trap and cause a 'feeding frenzy' but short enough for the bait to remain relatively intact and fresh. At no stage within the experimental period was the bait fully consumed between trapping sessions.

Mansfield *et al.* (1998) constructed decoys with aluminium foil wrapped with plaster of Paris gauze strips and captured five adult *Clemmys gutata* in 508 trap days with decoys present, compared to only 1 adult without decoys in traps. With such small capture rates it is difficult to determine whether the decoys were effective, however the major attractant for *E. macquarii* may be the movement and feeding of live decoy turtles in traps and constructed decoys probably have limited success.

It is possible that the presence of decoys may only concentrate the turtles into a few traps without attracting significantly more turtles. However, over the same period in 1995 and 1996, in the same lagoons and similar trapping regime, only 68 and 65 *Emydura macquarii* were captured respectively, less than the 82 turtles caught in the decoy study. The use of bait cages in hoop traps and the placements of turtles into traps are effective techniques to attract *Emydura macquarii* to baited hoop traps.

Although captured in small numbers in this study, it is curious that both *Chelodina* species present in the area avoided the traps with *E. macquarii* decoys present. *Emydura macquarii* are voracious and have very powerful jaws and it is highly probable that they out compete the *Chelodina* species for the ox-liver, especially *C. longicollis*, which is much smaller than *E. macquarii*. In contrast, *E. macquarii* is vulnerable in the Bellinger River catchment on the northern N.S.W coast because of possible competition with another shortneck turtle, *Elseya georgesi* (Appendix 1).

3.4.3 Conclusion

Emydura macquarii predominantly inhabit the thermally warmer and stable environment of permanent lagoons of the upper Murray River and the use of decoys in traps maximises capture success.

Chapter 4 Growth and Reproduction

4.1 Introduction

Understanding the relationship between body size and age is important for the development of demographic models. In turtles, body size can have a large influence on parameters such as fecundity because clutch size and frequency are positively related to body size in most freshwater species (Zuffi et al. 1999, Van Loben Sels et al. 1997, Iverson 1991a). Similarly, survivorship is positively related to body size, with nest mortality greater than 80% each year in most freshwater species and adult survivorship close 100% per year. Many demographic models of reptiles are based on size rather than age (Crouse 1999), yet these models still require a measure of the growth rate of a species because the components of the model rely on the amount of time spent in each size class (Cochran and Ellner 1992). Age and size at maturity represents an important transitional stage in demographic models, and most studies on freshwater turtles have estimated age at maturity specifically using species that display annuli on epidermal scutes as indicators of age and growth (Iverson 1991a, Wilbur 1975). Unless previously evaluated, growth annuli can be unreliable determinants of age, particularly as the individual ages (Cox et al. 1991, Galbraith and Brooks 1987). Only one study on Australian turtles has compared annuli against recapture data (Kennett 1996), and many studies use

growth annuli without evaluating their accuracy to determine age in relation to size (Parmenter, 1976, Chessman 1978).

Australian freshwater turtles generally conform to the typical reptilian growth pattern (Bury 1979) of rapid juvenile growth followed by a decline in growth rates as individuals reach maturity; growth of adult turtles is often irregular and indeterminate (Chessman 1978, Georges 1982, Kennett and Georges 1990, Parmenter 1976, Kennett 1996). The method developed by Fabens (1965) to fit recapture growth data to the von Bertalanffy model and derive age-size curves has been used to describe the growth of many freshwater turtles (Lindeman 1999, Jones and Hartfield 1995). Only two Australian species, *Chelodina rugosa* and *Elseya dentata*, have been compared with this model and the growth of both fit the model relatively well (Kennett 1996). The pattern of growth of *E. macquarii* in the Murray River (Chessman 1978) is broadly consistent with other Australian turtles (Georges 1982, Kennett 1996), although previous growth data were predominantly based on annuli to age animals without quantification of the potential error.

Annual variation in clutch size is well studied in birds (Forbes 1991, Hiom *et al.* 1991, Martin 1995, Young 1996, Korpimäki & Wiehn 1998, Wiebe *et al.* 1998) but, despite many studies on the reproductive biology of turtles (Congdon and Gibbons 1985, Fraser 1991, Booth 1998a, Kennett 1999, Zuffi *et al.* 1999), very few have concentrated on yearly clutch size differences (Etchberger and

Ehrhart 1987, Bjorndal and Carr 1989, Iverson 1991a, Iverson and Moler 1997). Food energy assimilated by an organism is partitioned into four areas: maintenance, growth, reproduction, and stored energy, but if food is limited, these organisms make trade-offs in allocating energy to these competing areas (Scott and Fore 1995). Many birds produce fewer offspring to maximise fitness in years when food is limited (Young 1996, Korpimäki & Wiehn 1998, Wiebe *et al.* 1998) because animals with parental care must predict future availability to feed their young, as well as allocate present resources to egg production. Clutch size of Eurasion kestrels (*Falco tinnunculus*) falls to about half when voles (*Microtus agrestis*) are in low numbers (Korpimäki & Wiehn 1998). In species without parental care, such as turtles, future availability of food is unlikely to contribute to the allocation of present resources to reproduction and food and resources may not be limited and influence reproduction in species that exploit many food sources in relatively stable environments.

In this chapter I determined whether annuli are a reliable index of age in *E. macquarii* in the Murray River and I developed an age-size curve. I also compared the growth trajectory using mark-release-recapture techniques and von Bertalanffy and logistic growth equations, to determine size and age at maturity. The possible relationships between body sizes, age at maturity and fecundity, as well as causes for clutch size variation, were investigated.

4.2 Materials and Methods

4.2.1 Data Collection

Turtles were captured and marked as described in chapter 2. The number of annuli present on the left pectoral plate (Sexton 1959) was initially used to estimate age, but it became clear that annuli were difficult to see, even in small turtles. As part of an experiment to determine hatchling survival (chapter 6), 1218 hatchling turtles were marked and released at the beginning of 1997 and 1998 into Bankview and Hawksview lagoons (see chapter 6) and as many were recaptured as possible over the total trapping period. Each hatchling's carapace and plastron length were measured. Recaptured turtles were re-measured (chapter 2), and the number of growth rings present on the left pectoral plate of the plastron was recorded. From each population, I plotted the plastron lengths of turtles captured during one season (September-April) and determined its growth rate (incremental changes in plastron length) if recaptured in the following season i.e., an index of one growth year. *Emydura macquarii* hibernate in the Murray River and grow very little over this period (Chessman 1978). I imposed a minimum growth interval of 274 days and a maximum of 427 days to ensure only one growth period of each turtle is represented. Each turtle's growth was represented once for the analysis i.e., if turtles were captured in multiple trapping seasons, the growth between the first two seasons were included in the analysis. Adult male and female turtles were analysed separately, but juveniles could not be easily

sexed so I assumed that juvenile turtles of both sexes grew at similar rates. From recapturing turtles of unknown age and recapturing the hatchlings released in 1997 and 1998, I determined the relationship between size and growth rate for *E. macquarii*. Regression analyses between plastron length (PL) and the natural log of growth rate (GR) were performed to determine the strength of the relationship. I applied the relationship between plastron length and growth rate to determine the age of each individual. The resultant ageplastron length relationship is based on known-age hatchling and juvenile growth and the growth of recaptured adult and juvenile turtles.

The von Bertalanffy and logistic models are asymptotic models that describe growth rate as a function of size (Fabens 1965, Schoener and Schoener 1978). The general form of the von Bertalanffy equation is given in the form.

$$L=a(1-be^{-kt})$$
 (4.1)

where: L= plastron length (mm) a= asymptotic length e= base of natural logarithms b= related to hatchling length, where b= 1-h/a (h=hatchling length) k= intrinsic growth rate t= is age

Fabens (1965) derived the growth-interval equation of the von Bertalanffy model,

$$L_2 = a - (a - L_1) e^{-k (dt)}$$
(4.2)

Where L_1 is plastron length at first capture, and L_2 is plastron length at recapture, and dt is time in years between capture dates. Growth data of turtles captured one or more trapping season apart were included in the

model. Growth trajectories are estimated from the growth of recaptures using non-linear regression of the interval equation to estimate the parameters a (asymptotic size) and k (growth coefficient). The parameter b in equation 4.1 (a constant derived from hatchling and asymptotic lengths-Dunham 1978, James 1991, Schoener and Schoener 1978) is calculated using the estimated values of a and k. Mean hatchling plastron length was determined from the 1218 turtles released during 1997 and 1998.

The general form of the logistic equation (Schoener and Schoener 1978) is:

$$L = a/(1 + be^{-kt})$$
 (4.3)

and the logistic growth interval equation for recapture data is:

$$L_2 = a L_1 / (L_1 + (a - L_1)e^{-k(dt)}$$
(4.4)

The parameters are defined as for equations 4.1 and 4.2 and the same procedures in solving the von Bertalanffy growth equation were applied to determine growth trajectories using the logistic model. Plastron lengths at capture and recapture, and time intervals between capture and recapture were used to fit to von Bertalanffy and logistic growth interval equations with JMP (SAS incorporated) non-linear least squares regression procedures. The model that returned the smallest residual mean square error (residual sum of squares/*n*) was considered to be the one that fitted the data best (Dunham 1978, James 1991, Schoener and Schoener 1978). Male *E. macquarii* were considered mature when their tail was visibly elongated and the smallest (PL) males at each site were determined. The plastron lengths of the 10 smallest males were used to determine mean size at maturity. Female *E. macquarii* lack the elongated and enlarged tails of males (Chessman 1978) and the ten smallest mature female *E. macquarii* were determined by palpating females for oviductal eggs from October through to December each year.

4.2.2 Reproduction

During the spring and summer months, intensive trapping occurred in each lagoon to determine the proportion of adult females that reproduce each year. All females captured were palpated in the inguinal region to detect the presence of oviductal eggs. Females were judged reproductive if (1) they carried oviductal eggs when palpated and/or (2) were nesting or returning to ponds with clear indications of a recent nesting attempt such as soil on the posterior carapace.

The nesting season generally lasts from late October to early December. The most intense nesting occurs early-mid November after the first major rainstorm. Turtles were found by driving around each lagoon during the day and night and generally each female was observed until nesting was completed. During intense nesting nights, once the female had begun laying eggs, she was identified if previously marked and the nest was marked by placing a small wooden stake (10 cm) 5 m north of the nest. In all cases nesting was completed despite my presence in the area. Turtles observed until nesting was complete were identified, weighed, and measured.

I determined the clutch sizes from females in Mulwala lagoon and Lake Mulwala during three nesting seasons (Chapter 2). Eggs from reproductive female turtles were collected by inducing oviposition (chapter 2). The total numbers of eggs per female and female plastron and carapace lengths were recorded. Females were again palpated after oviposition to determine whether the female retained some eggs. If eggs were still present in the female's oviducts, that female's clutch size was not included in the analysis. The relationship between body size and clutch size in both populations were compared using regression analysis. Despite palpating females after oviposition, a small but unquantified proportion of retained eggs may not have been identified, so mean clutch size may have been slightly underestimated.

Annual variation in individual clutch size was determined from turtles recaptured annually over the three-year period. Differences in clutch sizes over the three years were analysed using a one-way ANCOVA with repeated measures, using plastron length as a co-variate. The growth rates of these females were also compared over the same period with a paired t- test.

4.3 **Results**

4.3.1 Growth and Maturity

Growth annuli were extremely variable by age two. Twelve of the hatchlings released into Bankview and Hawksview lagoons in early 1997 were recaptured at the beginning of 1998. Ten of these hatchlings had one observable growth ring on shields of both the carapace and plastron and two hatchlings had no discernible increments. Forty-two hatchlings from 1997 were recaptured at age two in early 1999; 26 hatchlings had two annuli on their carapace and plastron, four had one annulus, 11 had no discernible annuli and one hatchling had three visible annuli. Thus, there is a 17% (2/12) chance of error in aging first year *E. macquarii* and the error in aging increases to above 36% (16/42) after two years. For these reasons, growth rates (in PL) of juveniles and females were solely determined from recaptures of intervals of one trapping season.

Hatchlings that were released in 1997 grew $40 \pm 1 \text{ mm PL}$ (SD) during the first year (n=12), and turtles that were captured in 1999 and aged two, were 68 ± 9 (SD) mm PL (n= 42) greater than their original size. The variation in first year growth rates was extremely small and second year growth was estimated by applying average first year growth (40 mm) to the initial PL of each hatchling captured in 1999 and determining the difference between the recaptured length (PL) and the estimated value for 1998. Hatchling and juvenile growth

is rapid but declines to less than 5 mm per year in individuals with a plastron length of 200 mm (Fig. 4.1).



Fig. 4.1. Relationship between growth rate and plastron length of juvenile and female *Emydura macquarii* fit to logarithmic least squares.

Based on recapture data and the relationship between growth and plastron length (PL), growth rate (GR) for females and juveniles is best defined by a logarithmic equation ($R^2 = 0.93$):

$$\ln (PL) = 5.4 - 0.05 (GR)$$
(4.5)

Growth of male *E. macquarii* declines linearly after maturity and males continue to grow beyond 200 mm PL (Fig. 4.2). Growth varies from 9 mm.yr⁻¹ to 2 mm.yr⁻¹ between 170 mm and 180 mm PL respectively and growth after maturity is best described by the linear equation ($R^2 = 0.72$):

$$PL= 214 - 6.7(GR)$$
 (4.6)



Fig. 4.2 Relationship between plastron length and growth rate of adult males E. macquarii

The size of one and two year old turtles are known from recapturing hatchlings released in 1997. The relationships between plastron length and growth rate is extremely strong, especially within female turtles (R^2 =0.93). By using equations 4.5 and 4.6, as well as mean hatchling size (27 mm PL), I developed a relationship between age and size (PL) (Table 4.1) by assuming that juvenile growth was the same for both male and female turtles, as it is in *Trachemys scripta* (Dunham and Gibbons 1990).

| Age | Predicted Size (PL) | Known Size (PL ± S.D) |
|-----|---------------------|-------------------------|
| 1 | 68.3 | $67.5 \pm 1 \ (n = 12)$ |
| 2 | 94.3 | $95.9 \pm 9 \ (n = 42)$ |
| 3 | 114 | |
| 4 | 130 | |
| 5 | 143 | |
| 6 | 155 | |
| 7 | 165 | |
| 8 | 174 | |
| 9 | 182 | |
| 10 | 189 | |

Table 4.1 Relationship between age and size of female *E. macquarii* predicted from equation 4.5 and mean hatchling size (27 mm PL). The third column is the size of hatchlings marked and released in 1997 and recaptured in 1998 and 1999.
The predicted sizes were similar to the actual sizes of turtles that were

released in 1997 and recaptured in 1998 (age 1) and 1999 (age 2).

The growth data of both male and female E. macquarii fit the von Bertalanffy

model extremely well. In all cases the von Bertalanffy model has smaller

residual mean square than the corresponding logistic model (Table 4.2),

indicating that the former is more appropriate for describing growth of both

male and female *E. macquarii* (Frazer and Ehrhart 1985, Cox et al., 1991).

| Model | a | K | RMS | MSE |
|---|------------------------|-----------------------------|--------------|--------------|
| Female | | | | |
| von Bertalanffy $(n=901)$ | 214 (2.8) | 0.20 (<0.01) | 5.04 | 25.4 |
| logistic (n= 901) | 206 (2.8) | 0.72 (0.02) | 14.37 | 207 |
| Male von Bertalanffy (n=487) logistic (n=487) | 208 (2.6) 195 (1.6) | 0.23 (<0.01) 0.84 (0.01) | 4.06 7.63 | 16.5 58.2 |

Table 4.2. Non-linear regression of recapture data fitted to the von Bertalanffy and logistic equations. *a*: asymptotic plastron length (\pm S.E), *k*: characteristic growth parameter (\pm S.E) (Schoener and Schoener 1978), RMS: residual error mean square, MSE: mean square error.

The von Bertalanffy model produced a curve that was extremely similar to the

predicted curve based on recapture data and known age individuals

(recapture/known-age model). For both male and female data, the curves

follow a similar trajectory, except near the female asymptote, where the von

Bertalanffy rate of growth declines much faster than the curve based on

growth rates and initial hatching size (Fig. 4.3).





The average plastron length at maturity for female *E. macquarii* is 187 mm and the ten smallest gravid females were between 175-195 mm PL in Bankview, 179-192 mm PL in Hawksview and 173-193 mm PL in Snowdon's Lagoons. Thus, according to the recapture/known-age and the von Bertalanffy equations, females mature between nine and 12 years (Fig. 4.3). Male turtles have elongated tails at an average plastron length of 147 mm based on the ten smallest males in each lagoon (141-152 mm PL at Bankview, 139-151mm PL at Hawksview and 147-155 mm PL at Snowdon's lagoons). Using the recapture/known-age equation, male *E. macquarii* begin to mature between five and six years (Fig 4.4). The von Bertalanffy equation predicts male E.

macquarii mature between four and seven months earlier than the

recapture/known-age equation.





The models were recalculated using only growth data of female and juvenile turtles captured and recaptured throughout the study period, excluding growth data of known-age hatchlings released in 1997 and 1998, to evaluate the importance of growth rates of young (small) turtles to the general shape of the growth curve. Growth trajectories are similar to the full model, except that it fails to predict the large growth rate of hatchling and juvenile turtles (Fig. 4.5). Hence asymptotic size (234 mm PL) is much larger and the growth

parameter (k) (0.1) is less than half that predicted by the full model.



Fig. 4.5 The relationship between age and size of female *E. macquarii*, excluding juvenile growth.

- Projected age-size curve based on growth rates and size (equation 4.5)
- **_** Growth curve of females and juveniles constructed from the von Bertalanffy equation.
- Growth curve predicted by the von Bertalanffy model without data of released hatchlings.

4.3.2 Reproduction

Average clutch size of *E. macquarii* in Mulwala lagoon is 21.1 ± 4.8 eggs (n=134

range= 11-35). Clutch size is positively correlated with PL ($R^2 = 0.71 p < 0.01$),

increasing by one egg for each 3 mm increase in plastron length (Fig. 4.6).



Fig. 4.6. The relationship between plastron length (PL) and clutch size of *E. macquarii*.

Females generally produce only one clutch per year with more than 86% of females gravid each year (Table 4.3). Some females can produce a second clutch per year, as up to 20.3% of females were gravid in mid-December. Thus, average clutch frequency per year is 1.09. However, this percentage may include some females producing a late first clutch; no gravid turtles were captured after December 19 in any year.

| Date | Location | Gravid turtles |
|--------------|--------------------------------|--|
| Oct/Nov 1996 | Mulwala lagoon | 93% (125/134) |
| Oct/Nov 1997 | Mulwala lagoon | 88% (111/126) |
| Oct/Nov 1998 | Mulwala lagoon Lake Mulwala | 94% (76/82) 92% (47/51) |
| Dec 1996 | Bankview | 20.3% (13/64) |
| Dec 1997 | Bankview | 12.3% (5/41) |
| Dec 1998 | Hawksview | 17.9% (7/39) |

Table 4.3. Percentage of female *E. macquarii* gravid at different locations on

 Murray River. (total gravid/total caught).

From 35 females recaptured over three years, mean clutch size in 1996 was 22.1 ± 4.7 eggs, fell to 19.7 ± 4.9 eggs in 1997 and rose to 23.7 ± 4.2 eggs in 1998. Clutch size varied significantly each year (F_{2,101} = 14.7 p< 0.001), but was always positively related to plastron length (Fig. 4.7). Clutch size fell significantly in 1997 (p<0.001), but the number of eggs produced in 1998 was not significantly different from 1996 (p=0.96). Growth rates between 1996-1997 and 1997-1998 were not significantly different (t_{34} =0.31 p= 0.76).



Fig. 4.7 Clutch size of 35 female *E. macquarii* captured between 1996-1998. Clutch size, relative to body size, fell significantly in 1997, but clutches in 1998 were similar those in 1996. Clutch size in 1996 ($R^2 = 0.65$) Clutch size in 1997 ($R^2 = 0.73$) Clutch size in 1998 ($R^2 = 0.62$)

Throughout 1996, daily temperatures were generally below average and rainfall above average (Fig. 4.8). Temperatures in the winter of 1997 were above average, as they were in the following summer, but rainfall was extremely low throughout 1997 and the beginning of 1998, and the upper Murray was declared a drought area in February 1998 (Bureau of



Meteorology 2000). In 1998, winter temperatures were below or close to

Fig. 4.8 Rainfall and daily mean temperature differentials between January 1996 and July 1998 for the Mulwala region. _____Difference between mean daily maximum temperature for a particular month and the overall mean monthly temperature (left y-axis). ____Difference between total rainfall for a particular month and the overall mean monthly rainfall (right y-axis). (Bureau of Meteorology 2000).

4.4 Discussion

4.4.1 Growth

The rate of growth of *E. macquarii* is rapid in hatchlings and early juveniles, decreasing towards maturity and declining towards zero after maturity. This general pattern of growth is not atypical of freshwater turtles (Bury 1979) and, although limited to relatively few studies, Australian turtles consistently conform to it (Chessman 1978, Georges 1982, Kennett 1996, Parmenter 1976). The von Bertalanffy model describes the data very well for both male and female *E. macquarii*. In contrast, the logistic model, which is a good representative of growth of other turtles and squamates (Schoener and Schoener 1978, Frazer and Ehrhardt 1985, Jones and Hartfield 1995), does not accurately describe the growth trajectory of *E. macquarii* (Figs. 4.3, 4.4). Both the Frazer and Ehrhardt (1985) and Jones and Hartfield (1995) studies included few data on juvenile turtle growth and both the logistic and von Bertalanffy curves are similar in shape when fitted with data from only the upper size ranges (Fraser and Ehrhardt 1985). Even so, the von Bertalanffy model predicts a distorted version of growth without data from smaller size classes. Using only recapture data from medium-large size classes of E. *macquarii*, the von Bertalanffy model failed to predict actual hatchling and juvenile growth (Fig. 4.6) and estimates of female size or age at maturity would be grossly over-estimated. Thus, for *E. macquarii* and presumably other species, it is necessary that individuals from all size classes be represented when fitting growth models because differences between particular models are most apparent in the smaller size classes, where growth is maximal. The absence of smaller size classes underestimates the value of k (growth parameter) and thus the growth rate.

The growth patterns of *E. macquarii* at other locations on the Murray are similar to the Albury populations (Chessman 1978), and all Murray populations are similar to the growth pattern of *E. krefftii* on Fraser Island (Georges 1982). Nevertheless, the decline in juvenile growth rate is much sharper in the Albury populations, as juvenile and young adult *E. macquarii* continue to grow more rapidly in populations further downstream (Chessman 1978). The difference in growth rate between upstream and downstream Murray River *E. macquarii* could be real or could relate to sampling technique. Previous data used to estimate the growth of *E. macquarii* have relied on annuli (Chessman 1978) which are unreliable in estimating annual growth and determining age, at least in the Albury populations of E. *macquarii*, as well as in other species (Cox *et al.* 1991, Galbraith and Brooks 1987, Stott 1988). *Emydura macquarii* near Albury do not have reliable growth annuli and within two years of hatching there is a 36% chance of error in estimating age based on annuli. Carapace and plastron annuli can be used to estimate growth and age only when annual periodicity of the annuli is established (Gibbons 1967), a condition that is clearly not met for *E. macquarii*. If conditions are harsh or growth rate declines much earlier than expected, two annuli may appear as one and growth and age will be underestimated (Iverson 1991a). The adaptation of the von Bertalanffy growth model allows an alternative method of deriving an age-size curve when mark-recapture data are available and the individuals cannot be aged.

The growth models are robust enough to estimate age of *E. macquarii* up until maturity but they are of little value beyond maturity and approaching the asymptotic size (*a*). Small differences in plastron length (~2mm) could occur from measurement error or plastron deterioration (Kennett 1996). Large

turtles generally grow irregularly when conditions are favourable and the relationship between age and size becomes irrelevant for larger sized animals (Cox *et al.* 1991, Kennett 1996). Longevity is impossible to estimate from growth curves because of the indeterminate growth of larger individuals, although both male and female *E. macquarii* appear to survive beyond 20 years. The von Bertalanffy growth curves developed for female (Fig. 4.3) and male (Fig. 4.4) turtles are limited to about 15 years before the slopes of the projections approach zero. The asymptotic size predicted for female *E. macquarii* by the von Bertalanffy is 214 mm (PL), although some individuals in the populations were over 230 mm and if growth were small and indeterminate beyond maturity, these larger individuals would be much older than 20 years.

Although I did not know the ages of older individuals, the creation of an agesize curve from the relationship between growth rate and size (Fig 4.1) was consistent with the predicted von Bertalanffy model. The fitted relationship between plastron length and growth rate was strong ($Q \ Q \ R^2 = 0.93$, $\sigma' \ \sigma' \ R^2 =$ 0.72), and the variation in first year growth was surprisingly small (Fig. 4.3). Hatchling turtles may maximise growth over the first year to obtain a size where predation pressures are reduced, as survivorship in turtles is related to age (Shine and Iverson 1995), or more precisely size. Mortality rates are extremely high in the egg and hatchling stages of many species, but predation rates generally decrease with increasing size (Tucker *et al.* 1999). I expect that predation pressures on two-year-old *E. macquarii* with a plastron length of over 100 mm is much lower than on a hatchling that is only one third of the size, as magpies even had difficulty consuming recently hatched turtles (chapter 8). Hence, rapid growth over the first year is subsequently reduced and the variation in plastron length of two year old turtles is much greater than after initial hatchling growth (Fig. 4.3).

4.4.2 Maturity

Females generally mature around 190 mm (PL), but can mature as small as 172 mm. Both growth curves based on annual growth rates and the von Bertalanffy model (Fig. 4.3) predict that females mature between 10 and 11 years but can mature as early as eight, whereas male *E. macquarii* mature around 150 mm (PL) and between five and six years of age. Chessman (1978) estimated that male *E. macquarii* mature at a similar age and female *E. macquarii* mature much earlier than in the present study. Counting annuli on smaller or younger *E. macquarii* is less erroneous than counting them on older individuals as younger turtles grow much quicker than older individuals and hence there is less chance of two annuli appearing as one. Thus, estimates of male maturity are similar between the two studies, but as growth rates decline towards female maturity, the error of using annuli to estimate age also increases.

Species that are widely distributed like *E. macquarii* (Cann 1998) show considerable differences in growth and maturation both between sexes and populations (St. Claire et al. 1994). Male painted turtles (Chrysemys picta) in northern North America mature at similar ages to those in the south, however female turtles in the south mature later and grow quicker than northern populations (St. Claire et al. 1994). Similarly southern female E. macquarii (higher latitude) in the Murray River mature much later than turtles in northern NSW catchments, which mature at much smaller sizes and between three and five years earlier than the Murray River form (Georges 1982, David Judge pers. com.). On both continents, turtles at higher latitudes may be constrained by the number of clutches that can be successfully incubated per year. Northern female painted turtles reproduce at most once per year, whereas southern females can produce several clutches over a summer (St. Claire et al. 1994). Emydura macquarii in the current study generally produce one clutch per year, consistent with other studies of *E. macquarii* on the Murray River (Chessman 1978). Body size influences clutch size in many freshwater turtles and a larger body size and faster growth may be favoured in females in higher latitudes so that they produce larger clutches but at a much lower annual frequency. Large female *E. macquarii* in the Murray River can produce up to 35 eggs (Fig. 4.6) and the average clutch size of 21 eggs is far greater than northern *E. macquarii* and *E. krefftii* in Queensland that produce between three and four clutches of four eggs throughout spring and summer (Georges 1983). Alternatively, at higher latitudes, winters are usually

longer and colder and by growing quicker to a larger body size may increase survival and fitness more substantially than a small increase in clutch size.

Female turtles at higher latitudes may mature later and reach larger body sizes than those turtles closer to the equator, but the relative sizes at maturity may not be considerably different. Reproduction is energetically expensive, as it requires resources that would have otherwise been directed into growth (Bernardo 1993), and the reduction in growth rate after maturity is possible evidence of this cost. If turtles are delaying maturity to maximise clutch size, the relationship between size at maturity and maximum size will be close to 1.0. The relationship between size at maturity and maximum size for most freshwater turtles is between 0.72 and 0.75 (see Shine and Iverson 1995) but female *E. macquarii* in the Murray River delay maturity, as the ratio is 0.80. Delaying maturity and producing a larger clutch may not maximise reproductive potential and would only favour species with high adult survival. If a long reproductive life is assured, maximising body and thus, clutch size, will increase reproductive potential despite foregoing smaller clutches several years prior to maturity. Survival of *Emydura macquarii* is described by a Type III survival curve, where hatchling and early juvenile survival is very low but increases significantly throughout the juvenile stage and adult females exhibit extremely high survival, with close to 100% surviving each year (chapter 6). High longevity and delayed maturity of E.

macquarii on the Murray River increases annual clutch size and maximises reproductive potential.

In contrast, male *E. macquarii* do not delay maturity, as the ratio of male plastron length at maturity (147 mm) to asymptotic plastron length (205 mm) is 0.72. *Emydura macquarii* are sexually dimorphic with females maturing at larger sizes and reaching greater maximum sizes than males. In the absence of male-male combat, a male that matures at a smaller size will reproduce much sooner than a male that delays maturity. The minimum size of male maturity would be only constrained by a minimum size to physically mate with large females (Kennett 1996), the ability to produce enough viable sperm and the physical constraints of an increasing body size. Evidence for the large cost of female reproduction is possibly shown by the growth of males after maturity (Fig. 4.2). Males are able to grow relatively consistently after maturity and the estimated asymptote (*a*) is close to the maximum male size, whereas the female growth asymptote is close to maturity (Table 4.2), suggesting that female turtles grow periodically only when conditions are favourable.

Environmental conditions may also influence age at maturity. If resources are low, growth and reproduction can be reduced. Lack of resources alone does not appear to influence age at maturity as the growth parameters (k) estimated from the von Bertalanffy equation, representing how quickly growth approaches the asymptote for both male (0.23) and female (0.20) *E*. *macquarii*, were comparable to many other species that mature earlier. For example, female *Kinosternum sonoriense* (Rosen 1987), *Chrysemys picta* (Zweifel 1989) and *K. subrubrum* (Gibbons 1983) all have growth constants between 0.17 and 0.22 (Shine and Iverson 1995), but mature between five and seven years of age. The age at maturity of female *Emydura macquarii* is at the upper end of ages for freshwater turtles, which generally mature at 7-9 years (*Chrysemys picta-* 7 to 9 years (Iverson and Smith 1993, Wilbur 1975, Mitchell 1988), *Trachemys scripta-* 8 years (Frazer *et al.* 1990b), *K. sonoriense-* 7 years (Rosen 1987)). Several larger freshwater turtles mature at age ten or greater, The American snapping turtle (*Chelydra serpentina*) is estimated to mature at 20 years and *Chelodina longicollis*, a species that is sympatric with *E. macquarii*, matures at 10 years (Parmenter 1976).

Although limited resources may not influence age at maturity of *E. macquarii*, ontogenetic dietary shifts may cause the reduction in growth close to maturity. Most juvenile turtles are carnivorous despite the adult form being omnivorous (Hart 1983), and adult *E. macquarii* predominantly consume filamentous algae (Spencer *et al.* 1998) and aquatic macrophytes (Chessman 1986). *Emydura macquarii* are less efficient at processing aquatic macrophytes compared to a completely carnivorous diet (Spencer *et al.* 1998) and the decline in growth rate may reflect a gradual change from a highly digestible carnivorous diet to one much less digestible. The change in diet may also lead

to a habitat shift, as a dietary shift in *Pseudemys scripta* parallels a habitat shift from feeding sites in shallow to deep water (Hart 1983).

Food limitation generally underlies much of the variation in life history traits in birds (Martin 1995), but possibly less so in *E. macquarii*. Brood reduction occurs when parents cannot match clutch size to available food and where random failure of offspring occurs (Forbes 1991). In freshwater turtles, resource availability prior to ovulation or during follicular growth could limit clutch size (Etchberger and Ehrhart 1987, Iverson 1991a), but a reduction in food availability should also result in reductions of other functions such as growth. *Emydura macquarii* ceases feeding in April when water temperatures fall below 16 °C (Chessman 1988a) and over-winters in the water (Tasker 1991, Spencer 1995). Follicles enlarge in early spring (September) and ovulation begins in late October in the Murray River (Chessman 1978). During spring, feeding and activity is usually low because water temperatures are still relatively cool (Chessman 1978), so only resources accumulated in the previous summer and autumn could contribute to follicular enlargement. If food were limited during summer 1996-97, a reduction in the growth rate would also accompany the reduction in clutch size. Growth and reproduction ceases completely in *Chelodina longicollis* when food availability is reduced (Kennett and Georges 1990). Importantly, the decline in clutch size of *E*. *macquarii* in 1997 did not coincide with a decline in growth rate, suggesting that food availability alone was not limited throughout this period. Besides

low pre-ovulatory parental investment for care of hatchling turtles (Congdon and Gibbons 1989), *E. macquarii* is a generalist omnivore that could exploit many food types if preferred items were unavailable (Spencer *et al.* 1998). There is a delay of at least three months before resources accumulated during summer and autumn are used for follicle growth and egg production. Temperatures were generally above average in the winter of 1997 (Fig. 2) and in a warm winter, energy and resources used for reproduction may be used for other metabolic processes, as *E. macquarii* is ectothermic and unable to feed in winter (Chessman 1978). Post-hibernation fat reserves of female agamids are mainly expended in the development of the first clutch (Lin and Cheng 1986) and the time between the end of hibernation and follicular development of *E. macquarii* is too short to increase clutch size by feeding. Thus, resources available for reproduction, not food availability alone, could reduce clutch size in turtles, without affecting growth.

An alternate explanation for a reduction in clutch size of *E. macquarii* is the influence of rainfall prior to oviposition. Rainfall is a cue for the onset of reproductive events of many arid-zone animals. The Greyback Finchlark (*Eremopterix verticalis*) in the arid zones of South Africa lays larger clutches within one week of rainfall (Lloyd 1999) and rain enhances survival, growth and possibly clutch size and hatching success of lizards in central Australia (Dickman *et al.* 1999). During 1997 and early 1998, Australia's weather patterns were under the influence of an El Niño episode, resulting in below

average rainfall across southern Australia, particularly during winter (Bureau of Meteorology 2000). The extended period of low rainfall and high temperatures during 1997 and into early 1998 (Fig. 4.8) led to drought conditions for most of the southern half of the continent in the 1997-1998 summer. The incubation period of eggs of *E. macquarii* is over 70 days and, with oviposition occurring in November, most eggs incubate in the hottest and driest period (Thompson 1983a, Cann 1998). Emydura macquarii may adjust clutch size depending on environmental conditions prior to oviposition because of potential incubation conditions in late spring and early summer. *Trachemys scripta* can adjust reproductive output by either ovulating more follicles or adding material uniformly to all follicles ovulated in a particular reproductive bout (Tucker and Janzen 1998). If winter and spring conditions are favourable, *E. macquarii* may produce more follicles than in dry and warm winters, where material used to produce extra eggs could be redirected into producing a smaller clutch of larger eggs to survive the dry summer. *Emydura* macquarii eggs can incubate in relatively dry conditions (Thompson 1988), but in years of drought, producing larger eggs that contain more nutrients and water could reduce the risk of desiccation. Similarly, spring rains may increase the proportion of female western box turtles (*Terrapene ornata luteola*) laying eggs in the summer, but in years with dry springs, turtles defer laying eggs completely, rather than reducing annual output (Nieuwolt-Dacanay 1997).

How *E. macquarii* could determine winter and spring rainfall levels in an environment with regulated water levels is unknown. Nesting of *E. macquarii* could be physically triggered by rain itself, as nesting occurs during rainbearing, low-pressure weather fronts, similar to *Pseudemydura umbrina* (Kuchling 1993). Perhaps long periods without rain or low-pressure systems prior to ovulation, combined with warmer winter and spring temperatures, may reduce clutch size of *E. macquarii*, increasing survival of eggs through harsh summer incubation conditions.

4.4.3 Conclusion

In conclusion, turtle populations that experience high adult survival usually delay maturity (see Shine and Iverson 1995) because growth, maturity and reproduction are intrinsically linked. In most turtle populations, the production of eggs may come at the cost of growth and, because clutch size is highly correlated with body size, a species with high survival should delay maturity to maximise lifetime reproductive output. Similarly, if survival of hatchlings and early juvenile *E. macquarii* is functionally linked to body size, rapid growth over the first few years could reduce mortality rates considerably. The von Bertalanffy model for growth predicts the trajectory of juvenile *E. macquarii* growth is extremely rapid, female maturity is delayed compared to males and the growth rate is extremely low after maturity. Variability in clutch size can be explained by body size, but it may vary greatly as a result of extrinsic factors. Individual variation in clutch size may

also relate to winter and spring rainfall levels and their potential impact on

incubation conditions.

Chapter 5

Fox Removal

5.1 Introduction

In this chapter I outline the methods used to reduce red fox numbers (Vulpes *vulpes*) to experimentally test whether predation by foxes is causing a decline in turtle numbers. Fox densities in Australia vary from 0.1-12 km² (review in Saunders et al. 1995), and control of foxes is usually implemented under agricultural or endangered species management. Accurate estimates of their densities are required to effectively manage for their impact (Saunders et al. 1995). Reductions of between 60% and 70% of fox population are achievable control objectives (Macdonald 1980, Coman 1988) and, in relatively small areas (~10 km²) with persistent control efforts, fox numbers can be reduced to near zero (Banks et al. 1998). Fox baiting strategies differ between states, but 1080 remains the most common poison (Thompson 1994). Sodium monofluoroacetate (1080) is the preferred poison of vertebrate pest control agencies because it is cost-effective, humane and safe to use (Thompson 1994). The poison acts on a relatively specific group of animals, with canids (dogs and foxes) among the most sensitive (Mcllroy et al. 1986). Australian native animals are generally tolerant to high doses of 1080, particularly in Western Australia where 1080 occurs naturally in many native plants.

Many studies on the impact of foxes in Australian ecosystems have used a combination of 1080 baiting and spotlight shooting to reduce fox numbers, but have failed to confirm that fox abundance had actually declined. Without persistent fox control efforts, foxes can re-invade areas following control programs (Newsome *et al.* 1989, Thompson 1994) and only recently have there been experimental attempts to measure the full impact of fox predation on prey in Australian ecosystems (Banks *et al.* 1998). In this study, two census techniques were used to estimate the activity of foxes in all sites, and to confirm that fox control reduced the numbers below those in non-removal sites. The aim of fox control was to reduce predation pressures by foxes on *E. macquarii* to evaluate their impact on the Murray River population.

5.2 Materials and Methods

5.2.1 Study Sites and Experimental Design

The fox removal experiment was conducted around the four Albury lagoons (chapter 2). Foxes were monitored around all sites in 1996. In 1997 and 1998, after the first turtle nesting season, foxes were removed from around Snowdon's and Hawksview lagoons (removal), whilst foxes were continually monitored around Bankview and Cook's lagoons (control). Each site was chosen randomly as a removal or control site.

5.2.2 Fox Abundance

Fox numbers were monitored in all sites from July 1996 to January 1999, predominantly by using spotlight counts conducted over four to seven consecutive nights each month between August and November and every second month between January and May. The transect around Bankview lagoon (Fig 5.1) was 6.0 km long, approximating a spotlight viewing area of 1.5 km² (based on spotlight projection of 300m). The Cook's lagoon transect was similar in length to Bankview (6.2 km-Fig 5.2), but because it was less circular, more area was covered (~2.5 km²). Both transects around Snowdon's and Hawksview lagoons (Fig 5.3 and 5.4) were over 7 km long, each approximating a viewing area of 3 km². Transects were searched from an open car window or from the roof of a moving vehicle travelling at 5-10 km.h⁻¹ with a single observer using a 100 W spotlight. Although transects were not straight and the habitat was open, it is unlikely that an individual would have been counted on more than one occasion per night. The spotlight areas were all relatively flat and movement of foxes could be observed for long distances and either the lagoon or the River usually bordered the viewing area. All animals spotted per night were included in the transect count. The mean of the 4-7 nights spotlighting each month per site was used to measure relative fox densities (Newsome et al. 1989). Estimates of the variance between nightly spotlight counts were not calculated, as counts cannot be considered independent samples.



Fig. 5.1. Spotlight transect around Bankview lagoon. Control (non-removal) site.

Transect — Fence Highway Water



Fig. 5.2 Spotlight transect around Cook's lagoon. Control (non-removal) site.

Transect Highway Water Murray River



Fig. 5.3. Spotlight transect around Snowdon's lagoon. Fox removal site.

Transect

— Fence

Murray River

Water



Fig. 5.4. Spotlight transect around Hawksview lagoon. Fox removal site.



5.2.3 Fox Removal

Fox numbers were reduced from the two removal sites between May 1997 (after the first nesting season) and January 1999. At each of the removal sites; approximately 48 commercial 35 g FOXOFF[™] baits, each containing 0.3 g of 1080, were buried along most fence lines, hill ridges or access roads at both sites (Figs. 5.3 and 5.4), in accordance Rural Lands Protection Board regulations i.e. at least 200m from public roads and households. Baits were laid 150-200 m apart and were buried 100 mm beneath a pile of loose soil to attract passing foxes.

Between May and October baits were laid for 7-10 days and checked daily, but between November and April baits were checked only every three days. The majority of baits were left buried between trips (monthly or 2 monthly), and were always replaced with new baits if they were not taken during that period. Despite a decline in activity, baits were continually taken (at a reduced rate) by reinvading foxes and foxes that consumed more than one bait before dying.

5.2.4 Monitoring Fox Populations

Once removal of foxes had begun, any foxes seen in the two removal sites were shot in the head using a low velocity .22 calibre rifle that made minimal noise. Less than a third of the animals seen were shot, as most were too far away or too difficult to shoot. The most effective control technique was 1080 baiting. All locals agreed to cease baiting and shooting around both removal sites from May 1996 to January 1997, however after this period locals sporadically shot foxes (local residents recorded number of foxes shot). Shooting and toxic baiting did not occur at both Cook's and Bankview lagoons, the two non-removal sites.

Non-toxic bait uptake has been used to provide an index of fox abundance (Thompson 1994). Each year (August), 26 (5 km) non-toxic baits were buried in the same vicinity where toxic baits were laid in the removal sites, and along most fence lines and access roads in the two non-removal sites. The number of baits taken after three days was used as an index of the activity of foxes.

5.3 Results

5.3.1 Fox Abundance: non-removal sites

Between June 1996 and November 1997, fox numbers in both Bankview and Cook's lagoons fluctuated cyclically with peak numbers in summer (November- January), and a decline in winter (June-August). For five months between December 1997 and June 1998, fox numbers in the non-removal sites declined to near zero but by August 1998 spotlight counts were similar to the two previous years (Fig 5.5).



Fig. 5.5. Density of foxes from spotlight counts around the non-removal (control) sites.

5.3.2 Fox Abundance: removal sites

Initial fox densities at the removal sites were similar to the non-removal sites, with approximately 3.0 foxes/km² at both Bankview (non-removal) and Snowdon's (removal) lagoons, and approximately 1.5 foxes/km² at Cook's and Hawksview lagoons.

1080 baits were laid from May 1997 until December 1998, but fox numbers had already declined from Snowdon's lagoon. With help from local residents, 18 foxes were shot in the general vicinity of Snowdon's lagoon in February 1998. Once baiting began, spotlight counts of foxes remained below 0.75/km² and were below 0.2/km² by November (turtle nesting period) in both 1997 and 1998 (Fig. 5.6).



Fig. 5.6. Density of foxes from spotlight counts around the fox removal sites.

Non-toxic bait uptake declined significantly in both removal sites after 1080 baits was introduced. Typically between 60% and 80% of non-toxic baits were taken in the three-night period in all four sites before foxes were removed. However, bait uptake declined to less than 15% in the removal sites over the same period in 1997 and 1998 (Fig 5.7).

The exact number of foxes removed is not known, but I shot 10 from Hawksview and four foxes from Snowdon's. Local residents of Snowdon's reported that over 50 foxes were shot after January 1997, but some of these foxes may not have been from the immediate area. Only six dead foxes were found throughout the study. 1080 baits can take up to 24 hours to work and, by this time, foxes can move several kilometres or die in their den.



Fig. 5.7 Proportion of non-toxic baits taken from all sites over a three-day period in August 1996, 1997, 1998.

5.4 Discussion

The two indices used in this study to measure fox density or activity remained substantially greater in non-removal sites compared to removal sites. In removal sites, spotlight counts fluctuated seasonally, with a low in winter (June) and a high in summer (January), but between November 1997, when fox numbers were increasing, and January 1998, fox numbers declined dramatically (Fig. 5.5). The drought in the Albury region at the beginning of 1998 resulted in much of the vegetation dying and rabbit and hare numbers also declined during this period (pers. obs.). The small numbers of rabbits that remained were observed feeding at all times of the day, whereas under normal conditions they are primarily nocturnal (Banks 1997). Rabbit population dynamics in temperate areas are strongly influenced by rainfall (Gilbert *et al.* 1987), and rabbits remain the staple prey of foxes (Newsome *et al.* 1989). Transient and resident foxes may have dispersed to areas where rabbit numbers were greater and more food was available. Cubs are born in August, weaned by December and disperse during early autumn (Banks 1997) but, because prey densities were low, juvenile foxes may have dispersed at an earlier age during summer. The large peaks (Bankview and Snowdon's especially) in fox numbers (Fig. 5.5 and 5.6) in summer 1996 are predominantly due to females foraging with cubs, and up to six foxes were seen together on two occasions.

Only one feral cat and no wild dogs were observed in all sites, and it is unlikely that the FOXOFF[™] baits had any affect on other species, native or feral, other than foxes. Bait presentation, particularly burying baits, reduces non-target consumption considerably (Thompson 1994). Each method to index fox numbers used in this study has its limitations. Spotlight counts can produce coarse but sensible assessment of population trends, although their use to measure absolute densities may underestimate the true densities (Thompson 1994). Despite efforts to minimize noise during spotlighting (low velocity rifle), resident animals may become shy and counts may only include naï ve or transient animals, thus underestimating the true population size. But assuming that this number is consistent across study sites, the number of observed foxes are representative of the proportion in each population.

Non-toxic bait uptake rates are reliable and capable of monitoring low density populations, as well as being a good technique for measuring the relative abundance of foxes (Thompson 1994). The ideal transects to measure fox activity require more than 60 baits (Thompson 1994), but my sites were limited to straight line transects of 26 baits (200 m apart). Single foxes are likely to take more than one bait and, with a small number of baits present, this index may overestimate the number of foxes present. Nevertheless, the low uptake rate in the removal sites in 1997 and 1998 (Fig. 5.7) suggests that fewer animals were present than in 1996, and certainly far fewer than in the removal sites.

The evidence from both spotlight counts and bait-uptake indicates that the removal campaign successfully reduced fox abundance at Snowdon's and Hawksview lagoons. By the second nesting season (November) in 1997, the relative densities of fox numbers were less than 10% of those in non-removal sites and were even further reduced by the nesting season in 1998. Through continual 1080 baiting, particularly in the four months before November, foxes were effectively removed from these sites. The full impact of reducing

foxes on *E. macquarii* populations is explored in the next chapter.

Chapter 6 Impact of Foxes and Population Model Analysis

6.1 Introduction

Predation by the introduced red fox on Australian freshwater turtle populations had been reported previously (Parmenter 1976, Green 1980), but it was not until Thompson (1983b) reported that 95% of turtle nests are destroyed along the Murray River in South Australia that foxes were considered a major predator of nests. Nevertheless, the impact that high nest predation has on the dynamics and growth of these populations, or on any other reptilian population in Australia, remains unknown. Recent studies on the impact of foxes on endemic Australian species have focused primarily on mammals and birds (Hornsby 1982, Booth 1987, Kinnear et al. 1988, Banks 1997, Priddel and Wheeler 1997, Banks et al. 1998, Du-Guesclin 1998), whereas most reports of predation on reptiles are incidental in dietary studies of foxes (Catling 1988, Triggs et al. 1984). The removal of the primary predator of an ecosystem to evaluate their impact has been confined to studies on small mammals (Norrdahl and Korpimäki 1995, Banks 1997), where population growth, increased survivorship and recruitment have been the key responses to predator control. These studies have focused on the functional responses of predator and prey numbers (Banks 1997, Korpimäki and Norrdahl 1998) that
result in a continual cycling of both predator and prey numbers over four to five year periods (Korpimaki and Krebs 1996).

Long-term information on the population dynamics of long-lived species are difficult to obtain, so population models are useful tools for determining key life-history components and guiding conservation management policies for these species (Heppell *et al.* 1996a). Demographic models have been developed to estimate the decline of many marine turtle populations and evaluate the future success of management strategies (e.g. Crouse et al. 1987, Crowder et al. 1995, Heppell et al. 1996b), and despite most conservation efforts focusing on one life stage, eggs on nesting beaches (Crouse et al. 1987), analyses of these population models suggest that survival of adult and large juvenile turtles is far more critical to population stability and growth than earlier stages. These models have been critical to the re-assessment of conservation efforts for marine turtles. In many countries, particularly the U.S.A, federal government law requires the use of turtle excluder devices (TEDs) on trawl nets to allow large turtles to escape and reduce sea turtle drownings (Crowder *et al.* 1995). This management strategy is far less costly and more effective than headstarting (captive hatching and rearing of eggs from nesting beaches). However, the accuracy of these models is solely dependent on the accuracy of data on annual survival, growth and fecundity of the life stages for a particular population.

Predation pressures from foxes may limit many turtle populations, similar to many threatened mammal and bird populations, but a decline in turtle numbers will be slow to become evident because of their longevity (Thompson 1993). Thus, Australian freshwater turtles have received little attention regarding population management except for the western swamp turtle (*Pseudemydura umbrina*), which is classified as endangered and protected in two lagoons in Western Australia (Ladyman *et al* 1998). I assessed the Murray River *E. macquarii* populations by determining their densities, size structures and survival rates, as well as evaluating predation pressures from foxes using a predator exclusion experiment. These data were in turn used to determine population stability and develop best management practices using demographic models.

6.2 Materials and Methods

6.2.1 Turtle Density, Size Structure and Survival

Nesting females were observed in November to determine nest predation rates from each lagoon between 1996 and 1999. Nests were observed daily from oviposition until early December and fortnightly thereafter for signs of predation, which includes eggshell particles close to the nest, a distinct hole in the ground from digging and scats. The predation rate was determined by dividing the proportion of nests destroyed by predators by the total number of marked nests. The proportion of hatchlings per clutch to complete incubation and emerge from the nest was also determined. In late January or early February, all marked intact nests were dug up and the number of dead or infertile eggs and hatchlings were recorded. Predation rate on hatchlings as they moved from the nest to the water was also determined from the release of hatchlings in groups of 10 from previously excavated nests (chapter 8).

Early juvenile survival was determined by the mark and release of hatchlings raised in the laboratory. Eggs were collected (chapter 2) from more than 75 gravid females in Lake Mulwala and Mulwala lagoon in November 1996 and 1997. A total of 281 hatchlings in January 1997 and 328 in January 1998 were marked and released into each of Bankview and Hawksview lagoons respectively. Hatchlings were recaptured as part of the routine trapping program for adults and minimum known alive divided by the total number released was used as an index of the survival rate at the end of 1999.

The sizes and survival of the juvenile and sex-specific adult populations in each lagoon were also determined. As age of *E. macquarii* could not be determined directly, turtles were classified as either juvenile or adult based on size and dimorphic characteristics at maturity (chapter 4). I used RELEASE, a program developed by Gary White at Colarado State University and available on the world wide web (<u>ftp://ftp.cnr.colostate.edu/pub/release/</u>), to generate survival (noted as ϕ) and recapture (trapability) (noted as p) estimates for each sex and size class. Data from each site was split into three trapping years with a year encompassing all trapping sessions from spring (September) in one year to autumn (April) in the following year. Encounter history files were created that included a listing for each turtle, coded for each time period as either '1' (captured), or '0' (not captured). In Capture-Mark-Recapture (CMR) studies, robust goodness of fit tests are available for interval specific survival Cormack-Jolly Seber models (Jolly 1965, Seber 1965, Seber 1986, Seber 1992). The goodness of fit of the general model for adult female, adult male and juvenile recapture data between sites were tested using the program RELEASE (Burnham *et al.* 1987).

The program NOREMARK (<u>http://canuck.dnr.cornell.edu/misc/cmr/)</u>, which uses the Lincoln-Peterson method (Caughley 1977), was used to estimate the sizes of *E. macquarii* populations within each lagoon. The lagoons were closed to the River or any other water body and, although rates of immigration and emigration were not determined, they were assumed to be very low because *E. macquarii* rarely leaves the water, except to nest or bask (Chessman 1978). The densities (per hectare of surface water, chapter 2) of each age and sex class were determined for each lagoon.

6.2.2 Impact of Foxes

The impact of the red fox, *Vulpes vulpes*, on *E. macquarii* was evaluated using the fox removal experiment (chapter 5). In 1995, the carcasses of all dead

turtles were cleared from around each lagoon, and during 1996 fox numbers were monitored around the four Albury lagoons (chapter 5). During 1996, the carcasses of dead turtles were collected during the nesting season (November) and predation on nests was determined. The surrounds of each lagoon were searched daily for two weeks for destroyed female turtles, primarily between 10 and 20 m away from the shoreline where the majority of nests are laid (chapter 7) and near fox dens where they may have been deposited. All carcasses were sexed and measured (chapter 2).

During 1997 and 1998, fox numbers were undisturbed around Cook's and Bankview lagoons while foxes were removed from Snowdon's and Hawksview lagoons. Fox numbers were successfully reduced around removal lagoons and nest predation and adult predation rates were determined around both control and removal sites each year (chapter 4).

6.2.3 Model Development

Square-transition matrices that contained survival, growth and fecundity values calculated for a one-year period for turtles were derived to evaluate the impact of foxes. The stage-based models had three classes: eggs and hatchlings (E/H), juveniles (J) and adult females (adult- A) (Fig. 6.1). Adult fecundity was calculated by determining the number of eggs produced each year around each lagoon by using estimated population size, the female size structure and the relationship between clutch size and body size. The clutch

frequency per year was estimated at 1.09 (chapter 4). The annual survival rates of egg/hatchlings, juveniles and adult females were used in the model (Fig. 6.1) and the duration times in each stage and fecundity were based on growth curves developed in chapter 4.



Fig. 6.1. Schematic diagram of the population model of *E. macquarii* showing the three life stages, egg/hatchling, juvenile and adult stages, and survival, growth and fecundity for each stage. An Egg/Hatchling progresses to the Juvenile stage in the second year and likewise a Juvenile matures and becomes an adult at 10. Only adult turtles can reproduce (>10 years).

6.2.4 Model Analysis

The stage-based matrix entries occur on the diagonal (P_i the probability of surviving and remaining in a stage, on the subdiagonal (G_i the probability of surviving and growing to the next stage) and on the top row (F_i fecundity) of the matrix. I assumed that all individuals within a stage are identical and that a fixed proportion of individuals grew into the next stage each year. Although survival rates will differ with age and size, especially with juveniles, I

assumed that the survival rates in the model were the mean survival rates for the duration of the stage i.e. juvenile survival is likely to vary considerably between year two and year 11, with the older juveniles likely to exhibit adult like survival rates. The finite rate of population growth, λ , is the annual multiplication rate for the model population given that mean survival, growth and reproductive rates remain constant, and that the population is at a stable age or stage distribution. The population growth term is related to the intrinsic rate of increase, r, where $r = ln(\lambda)$. The elasticity of a matrix parameter is the proportional change in λ following an increase or decrease in that parameter. The proportional sensitivity analysis uses the stable stage distribution given by the right eigenvector of the matrix, and the stagespecific reproductive values given by the left eigenvector of the matrix with the first-stage reproductive value set at 1.0. Reproductive values estimate the expected reproductive contribution of each stage to population growth (Crouse et al. 1987). I used the elasticity values to compare the relative impact of stage-specific survival, growth and fecundity on population growth. To calculate elasticities, I used MATHPAD to determine the stable stage distribution (w_x) and stage specific reproductive values (v_x) . The elasticity matrix ($E_{x,v}$), which shows proportional change in λ given a proportional change in each matrix parameter $(M2_{x,y})$ is given by:

$$\boldsymbol{E}_{\mathbf{x},\mathbf{y}} = \underbrace{\delta \log \lambda}_{\delta \log M2_{\mathbf{x},\mathbf{y}}} = \underbrace{M2_{\mathbf{x},\mathbf{y}}}_{\lambda} \times \underbrace{v_{\mathbf{x}} \times w_{\mathbf{y}}}_{\langle \mathbf{v} | W \rangle}$$

where $\langle v | w \rangle$ is the inner product of two vectors or Σ ($v_x \ge w_x$) (Caswell 1989). Elasticities can be interpreted as proportional contributions of each matrix parameter to the population multiplication rate, λ (de Kroon *et al.* 1986). I used the stage-based models to simulate the current predation pressures from foxes, as well as a model with reduced fox predation at each lagoon.

6.3 Results

6.3.1 Densities, Survival and Size Structure

Estimates of catchability of *E. macquarii* were similar for adults of both sexes. In each lagoon, 60% or more of adult turtles alive during the first year of the study were captured at least once in either the second or third year of trapping, although less than 50% of juveniles were captured during the same period (Table 6.1). An estimated 687 adult females inhabit Bankview, 550 females in Hawksview, and 535 females in Snowdon's lagoon. In contrast, more adult male turtles are estimated to inhabit Hawksview than in Bankview and Snowdon's lagoons (Table 6.2). More females than males are estimated to inhabit each lagoon. Based on population size estimates, only about 30% of the total population in Bankview, 40% in Hawksview and 40% in Snowdon's lagoons are male.

| | Bankview | Hawksview | Snowdon's |
|---------------------------------------|----------|-----------|-----------|
| Female | | | |
| • 1 st year recaptures (%) | 76.3% | 72.8% | 61.6% |
| • 2 nd year recaptures (%) | 61.3% | 64.8% | 60.5% |
| Male | | | |
| • 1 st year recaptures (%) | 75.5% | 73.4% | 67.3% |
| • 2 nd year recaptures (%) | 55.5% | 60.7% | 61.2% |
| Juvenile | | | |
| • 1 st year recaptures (%) | 40.9% | 50.0% | 34.4% |
| • 2 nd year recaptures (%) | 41.4% | 40.0% | 23.8% |

Table 6.1 Proportion of female, male and juvenile turtles captured in the 1^{st} year and then recaptured in either the 2^{nd} or 3^{rd} years of trapping, as well as the proportion of 2^{nd} year turtles captured in the 3^{rd} year of trapping.

| | Bankview | | Hawksview | | Snowdon's | |
|--|------------|--------------|------------|--------------|---------------|--------------|
| | Value | Range | Value | Range | Value | Range |
| Adult FemalesAnimals captured | 615 | - | 476 | - | 460 | - |
| RecapturedPopulation size | 425 687 | - 667-711 | 320 550 | - 528-576 | 276 535 | - 513-561 |
| Survival rate | 95.6% | 4.3% | 96.9% | 5.1% | 99.5% | 5.5% |
| Adult males | | | | | | |
| Animals captured | 273 | - | 318 | - | 275 | - |
| Recaptured | 175 | - | 209 | - | 180 | - |
| Population Size | 317 | 301-338 | 383 | 361-410 | 315 | 298-337 |
| Survival rate | 99.1% | 8.3% | 98.9% | 10.1% | 99.2% | 8.8% |
| Juveniles | | | | | | |
| Animals captured | 89 | - | 69 | - | 64 | - |
| Recaptured | 30 | - | 26 | - | 17 | - |
| Population Size | 135 | 112-171 | 94 | 80-119 | 110 | 85-157 |
| Survival rate | 67.4% | 34.3% | 77.7% | 18.5% | 69.8 % | 24.8% |

Table 6.2. Total numbers of turtles captured and recaptured throughout the study period. Estimated population sizes and survival rates of adult females, adult males and juveniles from each lagoon. Standard errors for survival and recapture rates and 95% confidence intervals for the estimates of population size.

Predation rates on nests were very high, with 93% (27/29), 85% (17/20) and 92% (23/25) of observed nests destroyed in 1996 around Hawksview, Bankview and Snowdon's lagoons, respectively. Foxes were removed from Hawksview and Snowdon's lagoons in 1997 and 1998, but predation remained at high rates, 83% (19/23) and 85% (11/13), around Bankview (non removal) lagoon over the same periods. Foxes were the major predators, although birds and water rats also destroyed nests.

All nests that were not destroyed were considered successful i.e. at least one hatchling emerged from the nest. Of 56 observed nests, 2.0 ± 2.0 eggs per nest around Bankview, 2.4 ± 1.7 eggs per nest around Hawksview and 2.2 ± 2.0 eggs per nest around Snowdon's lagoons failed to develop (Fig. 6.2). Similarly the proportion of hatchlings that failed to emerge from the nest was small (Fig. 6.2). Birds destroy 10% of hatchlings that emerge from the nest as a group (Chapter 8). The magpie (*Gymnorhina tibicen*) was the only predator of hatchling turtles.



Fig 6.2. Dead eggs or hatchlings remaining in nests. Shaded bars are the number of dead eggs and solid bars are the number of dead hatchlings remaining in the nest pooled across all sites.

Survivorship from oviposition to entry of the hatchlings to the water was higher at Bankview than any other lagoon (Table 6.3), but total mortality of eggs and hatchlings is greater than 87% around all lagoons.

| | Bankview | Hawksview | Snowdon's |
|-----------------------------|-------------|-------------|-------------|
| Predation | 84% | 93% | 92% |
| | (2.07/21.1) | (2.42/21.1) | (2.22/21.1) |
| Eggs failed to develop | 9.8% | 11.5% | 10.5% |
| | (1.47/21.1) | (0.68/21.1) | (0.95/21.1) |
| Hatchlings failed to emerge | 7.0% | 3.2% | 4.5% |
| Predation after emergence | 10% | 10% | 10% |
| Total Survival | 12.1% | 5.4% | 6.2% |

Table 6.3. Summary of survivorship of eggs and hatchlings. Proportion of eggs failing to develop and hatchlings failing to emerge from the nest (n/21.1) were based on average clutch size of 21.1 (chapter 4). Predation after emergence was based on group emergence value (chapter 8).

First year survival of hatchlings once in the water was difficult to determine due to the lack of recaptures of hatchlings released in 1996-1997. Twelve hatchlings released in 1997 were recaptured in 1998. Seven (2.5%) hatchlings from Bankview and five (1.8%) hatchlings from Hawksview were captured in 1998 and no hatchlings that were released in 1998 were recaptured in 1999. However a further 42 hatchlings that were released in 1997 were recaptured two years later in 1999: giving minimum survival to two years of 10% (28/281) in Bankview and 5%(14/281) in Hawksview lagoons. Estimates of adult (male and female) and older juvenile (< 2 years) survival passed goodness of fit tests for equal catchability (adult female model, χ^2 = 11.1, d.f.= 6, p= 0.09, adult male model, χ^2 = 2.8, d.f.= 6, p= 0.83, juvenile model, χ^2 = 6.5, d.f.= 6, p= 0.37). Survival of older juvenile turtles was estimated at 67.4% ± 34.3% in Bankview lagoon, 77.7% ± 18.5% in Hawksview lagoon and 69.8% ± 24.8% in Snowdon's lagoon (Table 6.2). The relatively large errors are due to the small population of juveniles in each lagoon and thus, low capture rates. Survivorship amongst mature adult male and female *E. macquarii* was very high, with more than 95% of adults surviving annually in each lagoon (Table 6.2).

Female and juvenile size distribution between each lagoon were statistically similar (Bankview v Hawksview: $\chi^2_{25} = 7.29 \text{ p} = 0.1$, Bankview v Snowdon's: $\chi^2_{25} = 11.80 \text{ p} = 0.988$, Hawksview v Snowdon's: $\chi^2_{25} = 7.80 \text{ p} = 0.10$). The majority of females were between 190mm and 260mm PL (Fig. 6.3a). Males were smaller than females, with the majority of the male population between 160 mm PL and 210 mm PL (Fig. 6.3b).

6.3.2 Effect of Removing Foxes

The removal of foxes reduced nest predation rates. When foxes were present at each lagoon in 1996, nest predation rates were between 85% and 93%, much higher than predation rates at Hawksview (52%) and Snowdon's (47%) lagoons when they were removed in 1997. At the same time nest predation rates remained high at both Cook's and Bankview lagoons when fox numbers remained unaltered (Fig. 6.4). Predation rates remained at similar levels around each lagoon in 1998 (about 50% at Hawksview and Snowdon's lagoons and 90% at Cook's and Bankview lagoons (Fig. 6.4)).



Fig. 6.3 (a) Size structure of female and juvenile *E. macquarii* in Bankview (n= 704) and Hawksview (n=545) lagoons. Size ranges are based on yearly growth rates (chapter 4) until maturity and 5mm increments thereafter (b) Size structure of male *E. macquarii* in Bankview (n= 317) and Hawksview (n= 383) lagoons. Size structure of Snowdon's is not shown for both male and female populations but it similar to both Bankview and Hawksview.





- ____ Hawksview fox density
- Snowdon's fox density
- Hawksview nest predation rates
- Snowdon's nest predation rate

(b) Fox densities of non-removal sites and nest predation rates at each site over the same period.

- ____ Bankview fox density Bankview nest predation rates Cook's fox density
 - Cook's nest predation rate

Left y axis of each figure is fox density and the right y axis is proportion of nests destroyed by predators.

Foxes and birds are the primary causes mortality for turtles inhabiting lagoons. Magpies take eggs and hatchlings, and foxes are the major predators of nests and they kill nesting females. Searches of the lagoons at the end of 1995 located remains of 35 turtles. These were not included in any analyses and their removal was to clear all remains from the lagoons to determine mortality rates in the subsequent seasons. Turtles found killed by foxes were females between 186 and 212 mm PL. Remains were often found close to fox dens and fox scats were often found in the vicinity of the carcass. Typically, foxes remove the head, legs and feet of the turtle, and leave the remainder of the body. Predation on nesting adult females also declined when foxes were reduced from Hawksview and Snowdon's lagoons. In 1996, the remains of 12 adult females were found around Snowdon's (2.2%), six at Hawksview (1.1%), seven at Bankview (1.0%) and three at Cook's lagoons. In 1997 and 1998, after foxes were removed, no remains were found around Snowdon's and Hawksview lagoons and six and seven dead turtles were found around Bankview and three and five remains were found around Cook's lagoon over the same period. Predation from fish and other potential aquatic predators is unknown.

6.3.3 Population Growth and Fox Removal

Only the Bankview population was sampled when foxes were present over the whole sampling period and at current levels of survival, fecundity, and growth (Table 6.4), the *E. macquarii* population is declining at 4.3% (r=-0.0429 λ = 0.958). I also modelled two other permutations where the survival estimates may have been weak, hatchling and juvenile survival. I increased hatchling survival from 10% predicted from the minimum known alive to a survival rate of 50% in the model for each population, which could be above the true value. The influence on population growth is small, with a small decrease to the predicted population declines compared to the original values. Similarly, the estimation of juvenile survival rates was surrounded with large variances (Table 6.2), so I increased juvenile survival to 90% in the model for each population. At this higher rate of survival, the models predict that the Bankview population will still decline.

Because most sampling of *E. macquarii* occurred when foxes were removed from Snowdon's and Hawksview lagoons, I assumed that foxes did not influence adult survival rates over this period, despite predation occurring on nesting females during 1996. Thus, permutations from the model of each population are slightly conservative. I reduced the nest predation rates to reflect post-removal values of both Snowdon's and Hawkview populations (section 6.3.1). The *E. macquarii* population in Snowdon's lagoon is predicted to increase at 3.3%(r= 0.033 λ =1.003) per year and stabilise in Hawksview lagoon (r=-0.004 λ =0.996) when foxes are removed.

| Stage | Bankview annual survival | Hawksview annual survival | Snowdon's annual survival | Stage duration (years) |
|----------------|--------------------------------|---------------------------------|---------------------------------|------------------------------|
| Egg/Hatchlings | 0.0075 | 0.0203 | 0.0304 | 1 |
| Juveniles | 0.674 | 0.777 | 0.698 | 10 |
| Adult | 0.956 | 0.969 | 0.995 | No Limit |

Table 6.4. Stages used in the models for *Emydura macquarii*, their annual survival estimates and duration. Estimate of egg/hatchling survival rate for Snowdon's lagoon was based on 7.5% of hatchlings surviving per year once they have entered the water (mean of Bankview and Hawksview).

6.3.4 Model Results and Elasticity Analysis

More juveniles are predicted to inhabit the populations when foxes are removed (Fig. 6.5), but the proportion of adults in the control site are not different from both populations where foxes are removed.



Fig 6.5 Stable stage distributions of three matrix populations for *E. macquarii*. The stable stage distribution gives the proportion of individuals in each life history stage once the population has reached a stable distribution and constant growth.

I calculated the proportional effect of changes in the model parameters on the population growth rate (λ) using elasticity analysis (Caswell 1989). The growth *E. macquarii* population in the upper Murray River are more sensitive to the probability of surviving and remaining in a stage (P) than to growth (G) or fecundity (F) (Table 6.5), particularly to survival of adults.

| | | Bankview | Hawksview | Snowdon's |
|-----------|---------------|-----------|-----------------|-----------------|
| | | (control) | (foxes removed) | (foxes removed) |
| Survival | Juvenile | 0.0048 | 0.0544 | 0.0199 |
| | Adult | 0.9890 | 0.8935 | 0.9528 |
| Growth | Egg/Hatchling | 0.0021 | 0.0174 | 0.0091 |
| | Juvenile | 0.0021 | 0.0174 | 0.0091 |
| Fecundity | Adult | 0.0021 | 0.0174 | 0.0091 |

Table 6.5. Elasticities of each matrix parameter in three population models of *E. macquarii*. Elasticity is the proportional change in the population growth rate (λ) following a change in the matrix parameter.

In populations where foxes were removed, elasticity values for adult survival were lower than in the Bankview population, where foxes were present throughout the study. In particular, the elasticity value of adult survival in Snowdon's lagoon was below 0.90 and the value for juvenile survival was over 11 times greater than the Bankview population of *E. macquarii*. The lower elasticity value for adult survival in populations where foxes were removed is due to the increase in juvenile numbers in the stable stage distribution, which are equal to, or greater than, the number of adults in the population (Fig. 6.6).



Fig 6.6 Stable stage distributions of the *E. macquarii* populations in Bankview, Snowdon's, and Hawksview lagoons. The proportion of egg/hatchlings from each matrix population was not included in this figure to show the difference in the proportion of juveniles in the population in fox removal sites.

6.4 Discussion

6.4.1. Catchability

Estimates of population size and survival are more accurate when a high proportion of the population is caught (Caughley 1977) and catchability depends on age, sex and capture techniques (Ream and Ream 1966, Wilbur and Landwehr, 1974). The high-intensity of the mark-recapture study resulted in high capture frequencies for both adult male and adult females turtles in each lagoon, but capture and recapture rates of juveniles *E. macquarii* were low (Table 6.1). Unfortunately, other trapping techniques, such as seine netting and snorkelling, were not successful in Murray River lagoons because of the large quantities of debris, fallen logs and turbidity. There is a possibility that a proportion of the population is shy of hoop traps and was not sampled. The size of this group is impossible to determine, although the proportion probably varies across age and sex groups. Biases due to trapping techniques have received little attention within studies of turtle populations but without quantifying the full extent of biases, demographic parameters determined from the trappable population may not fully represent the population as a whole. Burgin et al. (1999) concluded that fyke nets, which are similar to the hoop traps used in this study, are not biased against *Chelodina longicollis*, but their study was extremely small (<40 animals captured in total) and contained very few juveniles in the population, the group for which biases may be the greatest. For *Elseva georgesi*, a short-neck turtle that is morphologically similar to, and is sympatric with *E. macquarii* in the Bellinger River on the North coast of NSW (Appendix 1), hoop trap captures are biased against adult males (Table 3 of Appendix 1) with significantly more captured by hand whilst snorkelling than in hoop traps. The estimated male population size of *E*. *macquarii* in the Murray River were less than half that of the female population size in some lagoons (Table 6.2) and in a species that lacks temperature-dependent sex determination (TSD)(Thompson 1988), trap bias against male turtles is the most likely explanation for these differences. Handcaptured male *El. georgesii* were mainly caught in the middle of the Bellinger River. Thus, as hoop traps must be placed close to the banks of lagoons or rivers (chapter 2), sex differences in habitat use may explain the variation in capture rates rather than trap avoidance by males. Conversely, the trappable

female population is likely to be representative of the whole female population because by the last nesting season, greater than 80% of turtles observed nesting around each lagoon in 1998 were previously marked. Trap biases will severely underestimate population size but estimates of other demographic parameters, such as survival, are unlikely to be affected.

The three populations were essentially closed because connection to the River only occurs during large floods and *E. macquarii* is almost totally aquatic, only emerging to bask and nest (Chessman 1978). Trapping was designed to avoid the possibility of some individuals being exposed to more or fewer traps than others, yet home range differences among individuals would expose some turtles to traps more than others, and turtles may have learned to avoid the traps after their first capture. *Pseudemys scripta* and *Chrysemys picta* become more wary of traps after capture (Tinkle 1958, Sexton 1959). Nevertheless, goodness of fit tests indicates that the catchability (the probability of catching any individual in each particular age or sex class) remained constant throughout the study. Thus, the majority of individuals do not avoid traps once marked and released, as further indicated by the high recapture rate of adult male and female turtles (Table 6.1).

6.4.2 Survivorship and Population Growth

The general survivorship pattern (Type II: constant rate of mortality) describes life history characteristics of many turtle populations (Tinkle *et al.* 1981, Gibbons and Semlitsch 1982, Mitchell 1988), but *E. macquarii* has a classic Type III survivorship curve, where survivorship increases with age. Nest predation is high, with between 82% and 93% of nests destroyed annually, which is similar to the predation rates in South Australia where 95% of nests are destroyed (Thompson 1983b). Foxes are the major predator of nests, and nest predation rates halved when foxes were removed from Hawksview and Bankview lagoons (Fig. 6.4). Predation on the nests of most freshwater turtles is high (Burke *et al.* 1998, Iverson 1991a), but the predation rate on nests of *E. macquarii* is higher than many other species. For example, predation on nests of *Chelydra serpentina* and *Emydoidea blandingii* in Michigan was 70% (Congdon *et al.* 1987) and 63% (Congdon *et al.* 1983) respectively, and predation on *Phrynops hilarii* nests is 82% (Souza Bujes 1998). Similarly, 84% of nests of *Kinosternum subrubrum, Pseudemys concinna floridana* and *T. scripta* are destroyed each year (Burke *et al.* 1998).

Nest predation on *E. macquarii* in the Murray River may have increased significantly because of two major human impacts. Firstly, the majority of the Murray River floodplain has been cleared over the last 200 years since European settlement and are now pastures or open grassland for agricultural purposes and as such, most nests are laid in a habitat that is devoid of high grass and tree cover that may otherwise provide some protection against predators or environmental extremes (Wilson 1998). Secondly, the introduction of foxes to Australia may have increased nest predation rates significantly. It is impossible to know the predation rates before European settlement, let alone the major predators of turtle nests. Dingos, varanids and the thylacine may have been the major predators on the Murray River prior to European settlement (Thompson 1983b), but the combined interaction of land-clearing and the introduction of foxes over the last 200 years may have produced much higher predation rates because of the ability of foxes to detect nests (chapter 7). Nest predation accounts for most egg loss, as survivorship of eggs is otherwise very high. Most *E. macquarii* eggs that avoid predation complete the incubation period (Table 6.3), similar to *Chrysemys picta* (Tinkle *et al.* 1981) and *T. scripta* (Cabrera-Pena *et al.* 1996) where over 80% of eggs develop. An average of one hatchling per clutch survives the incubation period to nest emergence and water entry but, because predators usually destroy the whole nest, this number is likely to be dominated by siblings from a few clutches.

Although estimates of predation rates on nests are available for many species of freshwater turtle (Congdon *et al.* 1987, Mitchell 1988, Iverson 1991a), there are few studies that have estimated hatchling and early juvenile survival. Small turtles are often difficult to capture or are cryptic, avoiding traps and other capture techniques. Unfortunately, I had too few recaptures to estimate hatchling survival using Jolly-Seber methods, but the minimum survival rate of a hatchling *E. macquarii* over the first two years is between 5% and 10% in both Hawksview and Bankview lagoons respectively. The true survival rate is likely to be greater because of potential trap bias and secretive nature of juvenile turtles (Chessman 1978). Cumulative survivorship of a cohort of 125 Trachemys scripta hatchlings to age 4 was 0.18 and the majority of this mortality occurred in the first year (Frazer *et al.* 1990a). Growth of *E. macquarii* is rapid over the first few years (chapter 4) and, because survival is related to body size in many species (Iverson 1991b), the rate of survival of older juvenile *E. macquarii* is 70% in each lagoon. By age three, the survival rate of *K*. *flavescens* is greater than 80% and generally greater than 90% by the sixth season (Iverson 1991a). The extent to which body size influences juvenile survival rate is unknown. Survival over the first few years of life may be related to size (Swingland and Coe 1979); Survival in K. subrubum is related to size over first few years of growth but beyond the sixth year, body size is irrelevant to survival (Iverson 1991b). A similar survival/body size pattern would be expected with *E. macquarii* with survival increasing rapidly over the first few years of growth, so that by the late juvenile stage when growth is approaching the asymptote (chapter 4), survivorship is similar to adult rates.

Life history is a suite of coevolved characteristics, including age-specific survivorship, reproductive output (clutch size and frequency), age at maturity, and longevity, which can influence population parameters (Congdon and Gibbons 1990). *Emydura macquarii* has low and variable survival rates in early life stages, matures relatively late, is iteroparous and has a high adult survival rate. As survival of *E. macquarii* is not constant throughout life, the implications of a Type III survivorship pattern are significant. Iteroparity is favoured in species with Type III survivorship patterns, as adult survival rates are high relative to juvenile survival rates and there is a strong possibility that annual reproductive output will result in complete failure (Cody, 1971, Charnov and Schaffer 1973 Holgate 1967, Murphy 1968). Thus, iteroparity increases the probability of a species with a Type III survivorship pattern producing at least one viable clutch in their lifetime. Despite high annual survival rates and longevity of *E. macquarii*, there is little evidence for reproductive senility. Only a small proportion of female *E. macquarii* were unlikely to produce at least one clutch of eggs per year (chapter 4) and few females do not have some follicles developing each year (Chessman 1978). Reproductive senescence occurs in *Terrapene ornata* (Legler 1960b) and *Deirochelys reticulata* (Gibbons 1969) but unless studies occur over several years, the presence of reproductive senility may be attributed to variation in clutch frequency, as some females may forgo reproduction in a particular year (Gibbons and Greene 1978). Following on, variation in clutch size and frequency may be due to proximate causes such as environmental conditions (chapter 4) and resource availability, which might mask variations in reproductive parameters that are due to senescence (Congdon and Gibbons 1990). It is this variation in demographic traits that are important for determining the evolution of life histories (Congdon and Gibbons 1990). Whilst key demographic parameters, such as mean survival and mortality rates between populations, were determined, variation between

and among population parameters, such as the relationship between age and size at maturity could not be determined over a relatively short period. With further study over that focuses on the released *E. macquarii* hatchlings, individual and between population variation of such parameters can be determined.

Thompson (1983b) inferred that Murray River turtle populations were under pressure from nest predation by foxes because the population consisted of mainly older and larger individuals. Similarly, the female and juvenile size structures in my study are dominated by turtles with plastron lengths greater than 190 mm (ie. 11 or 12 years or greater, chapter 4). Yet with close to 100% of adults surviving each year and very little recruitment because of nest predation, the majority of the population sampled must consist of mature older individuals and the pressure on the population inferred from the size structure and nest predation rates may not be real.

On the other hand, species with Type III survival curves are susceptible to external pressures, particularly changes in adult survival. When adults suffer increased mortality, turtle populations are generally subject to overexploitation because of the low reproductive success each year (Congdon *et al.* 1983). *Emydura macquarii* populations, particularly on the Murray River, are susceptible to low rates of adult predation by foxes. The combination of high reproductive potential and survival rates of adult *E. macquarii*, as well as extreme nest mortality, has resulted in population stability predominantly relying on survival of adults, hence, an elasticity value for adult survival well above that for any other turtle (see Heppell 1998). Of elasticity values calculated for many freshwater and marine turtles, only the Australian eastern long-necked turtle, *Chelodina longicollis*, has a comparable elasticity value for adult survival, 0.83 (Heppell 1998). Age at maturity is strongly correlated with adult survival (Shine and Iverson 1995) and age specific elasticities are dependent on these two life history traits (Heppell 1998). *Emydura macquarii* (chapter 4) and *C. longicollis* (Parmenter 1976) mature at 10 years or greater and both have adult survival rates greater than 0.95 (Shine and Iverson 1995). Most North American species of turtle mature earlier and have lower adult survival rates than *E. macquarii* (Shine and Iverson 1995), hence, elasticity values for adult survival are much lower and range from 0.2-0.7. One exception is the snapping turtle (*Chelydra serpentina*), which has an elasticity value above 0.8 (Heppell 1998), but like *E. macquarii* it matures later than 10 years (Shine and Iverson 1995) and has an adult survival rate close 1.0 (Cunnington and Brooks 1996).

Densities of *E. macquarii* range from 30 turtles per hectare in Snowdon's lagoon, 95 turtles per hectare in Bankview lagoon and 114 turtles per hectare in Hawksview lagoon. The range in densities could relate to differences in composition and productivity of the lagoons despite their proximity to each other (Boon *et al.* 1990), but is more likely to relate to the physical structure of Snowdon's lagoon. The majority of Snowdon's lagoon is shallow (Tasker 1991) and in summer, over half of the lagoon dries up so that turtles are confined to deeper areas (Spencer 1995). The real density during these periods is closer to 90 turtles per hectare. Emydura krefftii are present at numbers of 87 turtles per hectare on Fraser Island (Georges 1982) and *C. longicollis* can reach densities of up to 400 turtles per hectare (Parmenter 1976). Following on, biomass densities of *E. macquarii* are also very high, albeit localised to lagoons and backwaters. Between 180 and 200 kg per hectare of *E. macquarii* occur in the lagoons of the upper Murray River, which is well above the average biomass of most freshwater turtles (see Iverson 1982). Emydura macquarii are omnivorous (Spencer et al. 1998), and the highest calculated biomass density for an omnivorous turtle is 282.6 kg.ha⁻¹ for *Pseudemys scripta* in a pond in Florida (Auth 1975), but the average biomass is well below 200 kg.ha⁻¹ (Iverson 1982). Perhaps the high productivity of Murray River lagoons and a broad diet combine to support a high standing crop of turtles.

6.4.3 Population Stability and Management

Although high densities of turtles implies robustness, or population stability, the populations are susceptible to minor reductions in adult survival. The stability of each population is not reliant on numbers alone and the annual productivity of *E. macquarii* in the Murray River is very low because of low recruitment and early stage survival rates, rather relying on the large standing crop of turtles to maintain population stability. Unfortunately a three year study is not long enough to calculate year-to-year variability in life history traits and population growth. Matrix models act as a window to demonstrate that, at current survival, growth and fecundity levels, populations of E. *macquarii* on the Murray River are over-exploited and declining at 4% per year, primarily due to predation by foxes. The models show that small reductions in adult survival, similar to the small number of nesting females destroyed by foxes each year, have a dramatic effect on population growth. Similar results are found with marine turtles, where incidental harvest by trawling industries has lead to loggerhead (*Carretta carretta*) population declines (Crouse et al 1987, Heppell et al 1996b). Mandatory use of turtle excluder devices on all shrimp trawlers (Crouse 1993) has reduced the number of strandings (dead turtles on shore) in south-eastern USA to the point where the population of loggerhead turtles will recover in 30-40 years (Heppell et al. 1996b). Similar effective management of E. macquarii on the Murray that give a high priority to eliminating mortality of adult turtles is required. The known source of adult mortality is predation by foxes and intense baiting and spotlight shooting have the dual effect of eliminating predation on nesting females and reducing nest predation rates by half. This dual reduction in predation rates not only has the effect of reversing the population decline, but also greatly increase the proportion of juveniles in the population, thus reducing the elasticity value, or importance, of the survival of individual adult turtles to population stability and growth.

A criticism of the usefulness of elasticity analysis is that the life stages with the highest elasticity values are inaccessible to management (Heppell 1998). Reducing fox numbers to manage *E. macquarii* populations increases both egg/hatchling survival by reducing nest predation and the important adult survival stage by reducing predation on nesting females. However, reducing foxes is costly and requires constant monitoring as transient foxes will quickly acquire the home range of any removed foxes (Thompson 1994). To minimise management time and cost, two priority areas are critical. Firstly, important habitat must be identified and secondly, the timing of baiting is crucial for management. Wide scale management options for the Murray River are discussed in chapter 9.

Emydura macquarii has evolved with delayed sexual maturity, low adult mortality and high nest predation. Foxes have placed these Murray River populations at risk, through predation on nests and nesting females, but because of the longevity of these animals, a reduction in numbers will take much longer than many mammal and bird populations under similar threats. Management strategies must be developed that identify high risk and important habitat and conserve adult turtles.

Chapter 7

Nesting Ecology

7.1 Introduction

Predators can influence a prey population directly by injuring or killing an individual, and the threat of predation can influence the behaviour of prey at different life history stages. Behavioural modifications, such as restrictions in movement, can have enormous impacts on reproductive success and ultimately influence prey density. For example, Eastern grey kangaroos (*Macropus giganteous*) in sub-alpine regions of Australia forage in open grasslands, close to forest refuge, but when foxes, which kill juveniles and harass females with young, are removed from the area, females feed in more open areas and access better quality food. Predation on juveniles is reduced because predators are removed, but fecundity increases because females can access better quality food (Banks 1997, Banks et al. 2000). These sub-lethal effects of predation are complex and affect prey on different levels, but its impacts on reptilian life history stages are poorly known. Eggs of the Australian freshwater turtle, *Emydura macquarii*, hatch synchronously and emerge from a nest as a group, diluting predation risk (chapter 8). Because predation on nests is extremely high in many turtle populations (Burke et al. 1998, Yerli et al. 1997, Brown and MacDonald 1995, Iverson 1991a, Congdon et al. 1983), there may be strong selective pressures influencing female nest site choice.

There have been few investigations of the nesting activities of Australian freshwater turtles (Kennett et al. 1993a, Kennett et al. 1993b), despite the attention paid to the reproductive biology of many North American freshwater turtles over the last 20 years (Alho and Padua 1982, Congdon et al. 1983, Congdon et al. 1987, Choo and Chou 1984, Ewert et al. 1994, Buhlmann et al. 1995, Nieuwolt-Dacanay 1997). Numerous theories have been proposed for possible nest site selection, particularly with sea turtles. Thermal properties (Stoneburner and Richardson 1981), composition and densities of beach vegetation (Mrosovsky 1983, Hays et al. 1995), microhabitat and slope (Mortimer 1990), inter-species competition (Whitmore and Dutton 1985) and human disturbance (Witherington 1982) may influence nest site selection. Temperature-dependent sex determination (TSD) is also suggested as possibly influencing nest site choice (Vogt and Bull 1984, Schwarzkopf and Brooks 1985, Davenport 1998, Bragg et al. 2000). The sex of most North American species of turtle is determined by the incubation temperature of the nest, so the location selected by a female to nest will greatly influence the sex ratio of her offspring and thus potentially impact on the fitness of the young and the dynamics of the population (Bobyn and Brooks 1994a, Rhen and Lang 1995). While such factors influence reproductive success and ultimately population survival, natural selection suggests that direct predation risk should be the ultimate driver of nest site choice by a female turtle.

Freshwater turtles have armour that protects them from many predators, but many only emerge from the water to nest and are susceptible to predation (Tucker et al. 1999). Turtles in the Murray River suffer extremely high rates of nest predation, primarily due to foxes (chapter 6). Female Murray Short-Necked turtles emerge from the water to nest in November each year and foxes destroy a small proportion of these females (chapter 6). If solely reducing predation risk drove oviposition, nesting would occur close to water to minimise the distance and thus, time searching for nesting sites. Similarly, predation on hatchlings is lower if they emerge from nests that are closer to the water, as the time and distance that hatchlings traverse on land is reduced (Congdon et al. 1983). Nesting close to the water may not maximise the survival of the nest and eggs, which may also drive nest site selection. Female freshwater turtles nest in heterogeneous environments on the banks of rivers and lagoons, and because habitat characteristics and nest microenvironments are functionally linked, nest site selection can have consequences for the fitness of her offspring (Weisrock and Janzen 1999). Nests in beach zones on the Florida coast suffered high mortality during Hurricane Andrew (Milton et al. 1994) and predation on nests generally increases closer to water (Zimmerman 1984, Martin 1988a, Martin 1988b). Similarly nest predation rates are increased when nests are closer to the shoreline because predators can search more thoroughly for nests by using a linear search pattern (Congdon et al. 1983).

The costs associated with predator avoidance may influence the response to the perceived danger and this adaptive 'decision making' occurs in both invertebrates and vertebrates (see review Lima 1998, Sih 1987). Foxes have replaced most native predators of turtles and their nests on the Murray River and despite only being recently introduced to Australia, freshwater turtles are long-lived and may have quickly associated foxes as a potential predator and modified their nesting behaviour accordingly. How prey assess predation risk is extremely complex. Freshwater turtles are generally wary upon emergence from the water and will return at any slight disturbance. Thus visual recognition of a predator may play a significant part in nest site selection. Alternatively, where predators are a significant source of mortality, turtles may use indirect methods, such as chemical recognition, to avoid encounters. Odour is an important means of signalling amongst nocturnal mammals and reduces the risk of predation by recognition of a predators' presence (Ward et al. 1997, Weldon 1990). An innate response to a predator cue occurs if the two species have co-existed over evolutionary time (Ward et al. 1997), which Murray River turtles and foxes obviously have not because foxes were only introduced to Australia approximately 130 years ago (Saunders et al. 1995). However, Nolte et al. (1994) argued that the response-provoking component in one predator's odour might invoke a similar response with others in a prey not necessarily having an evolutionary association. Thus turtles may respond similarly to fox odour as they may to native predators, which were common prior to European settlement.

In this chapter, I show that sub-lethal impacts of predation have negative effects on the reproductive success of *E. macquarii*. By comparing nesting behaviour of female turtles between non-removal and removal sites, I determined whether movement of nesting turtles is restricted by the threat of foxes and secondly, whether any restriction of movement and access to resources affects hatching success and nest emergence.

7.2 Methods

7.2.1 Nesting Habitat

Nocturnal and diurnal searches for nesting female *E. macquarii* began during storms around the two non-removal sites near Albury-Wodonga (chapter 2) and two areas near Lake Mulwala (chapter 2) in November 1996, 1997 and 1998. All effort was made to not disturb females emerging from the water or during nesting; once the turtle had begun to lay eggs, she seemed oblivious to my presence. Emerging females would return directly to the water if discovered and turtles that were preparing the nest would cease until I was out of view. Nesting females were observed using binoculars (Tasco 8x21) or a night vision scope (Starlazer). Seventy-one females were observed over three years until they had finished nesting and returned to the water and their nests were marked by placing small wooden stakes or easily recognisable sticks five meters due north of the nest. Nests were observed daily for two

weeks and again four weeks after being constructed. A nest was considered successful, i.e. avoided predation, if it had not been destroyed four weeks from being constructed. Each nest was classified either intact or destroyed and I recorded whether each nest was constructed at night or day, as well as the weather conditions at the time of nesting (rain or dry). I measured the distance of the nest to the closest woody vegetation, distance to the water and distance to nearest nest. Soil type of each nest was classified as either dirt or sand as there were clear boundaries between the two types of soil at each site. Principal components analysis (PCA) was used to reduce the number of continuous (distance to water, distance to nearest nest and distance to nearest tree) nesting habitat variables to one or two principal factors. The principal components were then placed into a general linear model with the rest of the habitat variables and ANOVA was used to determine differences between the habitat types of destroyed and intact nests.

7.2.2 Predator Detection of Nests

Two areas around Lake Mulwala were used to determine whether foxes were discovering nests by the chemical cue of eggs and/or using slight soil disturbances of a recently constructed nest. Four treatment groups were used for the study: 1. eggs with disturbance to represent a freshly dug turtle nest 2. eggs with minimal disturbance, to represent an older nest 3. disturbance without eggs4. minimal disturbance without eggs. Ten samples of each treatment were allocated randomly to each area, with each 'nest' at least 50 m
apart to avoid density-dependent predation. For the first treatment group, a flask-shape nest was dug and 10 eggs were placed carefully inside the nest. An earthen plug was created from the wet soil excavated and the soil was flattened by hand. The second nest was created similarly with 10 eggs placed into the 'nest', however all effort was made to not disturb the grass and topsoil and all soil dug out was removed from the area. The third and fourth treatments were created by the same methods as the first and second treatments respectively, however no eggs were placed into these 'nests'. This experiment was first done with quail eggs in 1996 and again with *E. macquarii* eggs in 1998.

7.2.3 Nesting Behaviour and Predation Risk

Each year, I measured distance to water, nearest nest and closest tree of nests constructed while observing females nesting around both fox removal and non-removal sites, as well as all other nests (destroyed or intact) discovered subsequently. I compared these distance measurements between sites and nests at removal sites in 1997 and 1998 were considered low predation risk areas and nests in non-removal sites were high-risk areas.

7.2.4. Detection of Predators

To separate chemical or olfactory detection of predators and visual detection, I used islands in Lake Mulwala on the Murray River. In 1998 I characterised and plotted the position of nests on an enlarged topographic map for 10 of the islands. In November 2000 (less than 24 hours prior to nesting), I placed fox bedding and faeces around the shorelines and the main nesting areas of two of these islands. Similarly, I placed the bedding and faeces of a native predator (Eastern Quoll-*Dasyurus viverrinus*) that was present in the area prior to European settlement around two other islands using eastern quoll bedding and faeces. Two control islands were also used, where clean bedding was placed around the islands. I used distance to nearest nest to compare densities of nests on each island between years.

7.3 Results

7.3.1 Nesting Behaviour

The majority of *E. macquarii* nest in mid-November and are triggered to nest by storms and rain. Nesting occurred after November 8th, but some females nested after rain in late October and early November. In 1997, no major rainfall or storm activity occurred until late November and no females were found nesting until this event. Turtles emerged from the water at all hours, however peak numbers occurred immediately after rain began to fall and throughout the following night. Only a few turtles were found nesting by the third day after rain activity. Rainfall over the next week after a major storm would also trigger females to nest. Females take between half and hour and three hours to nest from the time of emergence from the water until she returns to the water, with the majority of females taking 45-60 min. The proportion of time allocated to locating a nest site and oviposition is similar. Females will often begin to construct a nest but abandon it and continue searching for suitable sites; some females will do this at least four times before completing a nest. After oviposition the female covers the nest with an earthen plug and disguises the nest by raising the plastron with her back legs and allowing it fall on the nest and surrounding areas. Goode (1967) termed this process 'ramming' and it usually continues for 20 minutes before the female returns to the water. Females returning to the water often appear slightly disorientated particularly those farthest away from the water. All head in the general direction of the water, however females rarely enter the same spot from where they emerge.

7.3.2 Nest Habitat

Of 71 nests, predators destroyed 52 leaving only 19 were intact after four weeks of incubation. The first two principal components accounted for 95% of the variance, PC1 accounting for 76% of the variation and PC2 accounts for 19% of the variation. PC1 represents increasing distance from water (95% of variance of PC1) and PC2 mainly represents an increasing distance from tree (82% of variance of PC2). Although intact and destroyed nests plotted in terms of the first two principal components (Fig. 7.1) indicates that there is considerable overlap in habitat, the majority of intact nests were neither close to trees or water. Most nests destroyed by predators were close to water and trees, although some nests away from water were also destroyed.



Fig. 7.1. Ninety-five percent confidence ellipses for habitat distance measures (described by principal components analysis) of intact and destroyed nests.

The majority of intact nests were found in a small distinct range between 15 m and 35 m from water (Fig. 7.2), as well as 10 m further away from neighbouring nests compared to nests destroyed by predators (Fig. 7.2).





Time of day and rainfall when the nest was constructed did not influence whether the nest was intact or destroyed, although soil type significantly influenced predation rate ($F_{1,65}$ = 15.2 p<0.001). Approximately half of the intact nests were constructed in sand compared to less than 20% of destroyed nests (Fig. 7.3).



Fig. 7.3. Percentage of intact and destroyed nests constructed in soil (filled bars) and sand (open bars).

Birds and foxes were the major predators of nests. Birds used their beak to create a distinct hole into the nest and usually swallowed eggs whole. On most occasions the nest was not completely destroyed by birds but usually within 24 hours all eggs were destroyed. Nests destroyed by birds and foxes were easily identified because birds left a small hole with little or no dirt surrounding the nest, whereas foxes usually left a combination of tracks, faeces and remaining eggshells. Foxes also left 'digging' mounds of dirt surrounding the nest. Water rats (*Hydromys chrysogaster*) destroyed two nests. The remains of nest destroyed by water rats had characteristics of nests destroyed by both birds and foxes, with a small circular hole surrounded by small mounds of dirt, tracks and/or eggshells. The Australian magpie was the major avian predator and was observed swooping from trees almost immediately after females had left the nesting area. Of the nests constructed during the day, the average distance away from trees of destroyed nests was 12.5 ± 12.7 m compared to 53.4 ± 14.8 m for intact nests (Fig. 7.4).



Fig. 7.4. Distance from nearest tree of destroyed and intact nests that were constructed during the day. (\pm S.D.)

7.3.3 Predator Detection of Nests

Only foxes destroyed nests in the predator detection experiments, with 70% of disturbed quail and 80% of disturbed turtle egg nests destroyed (Fig. 7.5). The proportion of destroyed nests with eggs and minimal disturbance, as well as nests with no eggs and disturbance were similar with both types of eggs present, however, nests with no eggs and minimal disturbance had low rates

of predation. Foxes appear to detect nests by both chemical detection of eggs and slight soil disturbance because nests with eggs and minimal disturbance, and nests without eggs but disturbed (disturbance) were destroyed far greater than nests without both eggs and disturbance (Fig. 7.5).



Fig. 7.5. Percentage of turtle (open bars) and quail (filled bars) egg nests destroyed in the predator detection experiments.

7.3.4. Predation Risk and Changes in Nesting Behaviour

Nest predation and direct predation on nesting females decreased significantly when foxes were removed (chapter 6). Nest site selection by *E. macquarii* also altered when foxes were removed. In 1996, female *E. macquarii* generally nested between 16 m and 20 m from water at each lagoon, but females nested much further from water once foxes were removed (Fig. 7.6). Conversely, female turtles nested at similar distances, or even closer to the water, in non-removal sites (Fig. 7.6). Female turtles utilise larger nesting areas when foxes are removed, and thus nests are less clumped and are further away from trees, which are generally close to bank (Fig. 7.6).



Fig. 7.6 (a). Mean distance of nests to the water of nests constructed around both removal and non-removal sites. **(b)** Mean distance of nests from the nearest tree in removal and non-removal sites. $(\pm$ S.E.)

A large proportion of nesting habitat at or close to the shoreline of most lagoons is river sand. Of nests not destroyed by predators, more eggs and hatchlings failed to complete incubation and emerge from the nest in nests constructed in sand than those constructed in soil (Fig. 7.7).



Fig. 7.7. Mean number of eggs and hatchlings per nest that failed to complete the incubation period in nests constructed in sand and those constructed in sand. (± S.D.)

7.3.5. Detection of Predators

Nest densities on the two islands in the fox treatment were not significantly different between years (t_{67} = 0.76 p= 0.22 and t_{87} = 0.32 p= 0.38) and the positions of nests were also similar (Fig. 7.8). However, densities of nests in the quoll treatment were significantly different between years (t_{85} = 4.65 p<0.001 and t_{127} = 6.07 p<0.001), as the majority of nests constructed in 2000 (after material with quoll faeces and bedding was spread throughout the island prior to nesting) were concentrated around the 'easy' access points, where the majority of turtles emerged to nest (Fig. 7.8). The densities of nests on the control islands were not significantly different between years (t_{92} = 0.57 p= 0.28 and t_{107} = 0.31 p= 0.38).



Fig. 7.8. Open circles are position of nests constructed on two islands in 1998. Closed circles are nests constructed after **(a)** quoll faeces and bedding was scattered throughout the island and **(b)** fox faeces and bedding was scattered throughout the island.

7.4 Discussion

Predation is an important process in many systems (eg. aquatic systems), but rarely has it been considered an important evolutionary process in reptiles (Downes and Shine 1998, Downes and Shine 1999, chapter 8). However, I have shown that the Murray River turtle, *E. macquarii*, modifies nesting behaviour in response to predation risk by foxes, which detect nests through certain chemical and habitat variables. Female turtles that construct nests a medium distance away from the water, and trees during the day and in sand are more likely to be left intact than nests in other areas. Nests that are not in the immediate vicinity of another nest also have a greater chance of survival. However, the trade-off is that females that locate their nests away from water, and hatchlings emerging from these nests, must spend more time moving overland and hence will incur greater predation risks and energy expenditure than those associated with nests located nearer to water (Congdon *et al.* 1983).

The majority of nests located close to water are more likely to be destroyed for two reasons. Firstly, predators can use the shoreline to search for nests more completely in a linear pattern than in two-dimensional areas such as the open fields (Congdon *et al.* 1983). Secondly, the probability of a nest being close to another nest is greater close to the water than further away and predators will search more intensely if there is a large density of nests in a particular area. Similarly, nests of *Chrysemys picta marginata* (Christens and Bider 1987) and *Chrysemys picta bellii* (Legler 1954) have a reduced predation rates when located away from ponds. In contrast, nests of both Emydoidea blandingii (Congdon et al. 1983) and Chelydra serpentina (Congdon et al. 1987) located further from water in southeast Michigan do not accrue such advantages. The cost for predators of searching a larger area may be offset by the increased probability of encountering longer trails left by females as they move from marshes to nest sites (Congdon et al. 1983). However, both studies (Congdon et al. 1983 and Congdon et al. 1987) were conducted on turtles that were

nesting in the same areas and it is possible that predators could detect nests of both species equally well. Intact *E. macquarii* nests are usually located within a small range of distances away from the water (Fig.7. 2a), possibly because nests located further away were closer to fox dens and more likely to discovered, as well as being closer to paddock fences which foxes use to traverse between areas (Thompson 1994).

In populations of cryptic nesting birds that do not defend their nest, the success of a nest generally decreases with increasing density of nests within an area (Hoi and Winkler 1994). The fate of an individual nest is linked to the fate of its nearest neighbor because some predators exhibit area-restricted searching behaviour (Lariviere and Messier 1998). Predators increase their hunting effort in an area where nests are commonly encountered (Burke *et al.* 1998), and once a nest is uncovered and destroyed, it becomes more visible to other predators and they may increase their searching activity (Lariviere and Messier 1998). Nests of *E. macquarii* located away from other nests (low-density) were discovered less often by predators than those in higher density areas (Fig. 7.2b), but distance to nearest nest accounted for only a small part of the total variance of the PCA. Thus, nest predation alone is not a simple function of density and hence unlikely to be a specific predictor of nest predation (Burke *et al.* 1998).

Most predation on turtle nests occurs within a day or two after the eggs have been deposited, and often within a few hours of construction (Burger 1977, Christens and Bider 1987, Congdon *et al.* 1983, Congdon *et al.* 1987, Legler 1954, Tinkle *et al.* 1981). Similarly, *E. macquarii* nests are often destroyed within seconds of the female leaving the area. Birds could only visually detect nests by observing females constructing them, as they never destroyed nests constructed at night and nests not detected immediately, remained intact or were later destroyed by other predators. Furthermore, the majority of nests destroyed during the day were oviposited near trees, where birds could observe nesting females (Fig. 7.4). Foxes detected nests by both chemical cues from the eggs and slight soil disturbance (Fig. 7.5) and turtle nests would be more susceptible to fox predation in the first few hours after nesting because the soil is freshly disturbed, enhancing olfactory recognition of eggs and the presence of female secretions.

Nest predation rates are extremely high with between 85% and 95% of nests destroyed in the upper Murray (chapter 6), but when foxes were removed from two sites, predation rates decrease to less than 50%. High nest predation rates in birds drive many life history traits, including clutch size and frequency (Martin 1995), and may also drive nest site choice. In response to high risk of nest predation, Tengmalm's owls (*Aegolius funereus*) shifts nest holes and increases breeding dispersal (Hakkarainen *et al.* 2001). In contrast, *E. macquarii* shifts nesting behaviour in high predation risk areas by nesting

closer to water, where the probability of nest predation is significantly increased. In high predation risk areas, the majority of nests are constructed in a narrow range between 15m and 20m away from the shoreline (Fig. 7.6), the region where most nest predation occurs (Fig. 7.2). Although this change in behaviour may appear to further decrease reproductive success, it may relate to direct predation pressure from foxes. Because foxes destroy a small proportion of nesting females ($\sim 2\%$) each year and many others have marks on their carapace and plastron, suggesting unsuccessful predation attempts, this area (15-20 m from the water) is where the influence of direct predation risk outweighs any preferences for nesting habitat. In lower risk areas, nests are constructed between 25 m and 30 m away from the water, where nest predation is less likely to occur (Fig. 7.6). The Murray River floodplain is predominantly used for agricultural practices and trees are predominantly situated in riparian zones, thus high nest predation rates are compounded in high-risk areas because nests are constructed closer to trees (Fig. 7.6) and predation by birds is increased.

Furthermore a change of nesting behaviour in areas of high predation risk reduces reproductive success through a reduction in hatching success and nest emergence (Fig. 7.7). Sand is not a common soil type in the nesting area and is mainly found close to the shoreline or where lagoons previously flowed, but nests located in sand had a much greater chance of avoiding predation than those located in grass and dirt (Fig. 7.3). Sand had very little grass associated with it, and because it was much looser than dirt, a nest would be much easier to disguise from predators. Foxes use both olfactory and possibly visual cues of disturbed soil to detect nests and, because sand is much looser than the soil, material secreted during oviposition and the moisture of the nest may evaporate much quicker, and hence be less detectable to predators. Although nests created in sand have a better chance of avoiding predation, it is not advantageous for incubation and hatchling survival. Hatchling survival and emergence is considerably reduced when nests are constructed in sand compared to soil (Fig. 7.7), similar to *Chrysemys* picta bellii eggs in artificial nests of sand that dehydrate quicker than eggs kept in clay (Legler 1954). With very little vegetation associated with sand, the incubation temperature range may be much larger than nests associated with soil and grass. Embryo survival in nests of *Kinosternum baurii* without vegetative cover is considerably reduced, because temperatures reach the thermal maximum more often than in nests with cover (Wilson 1998).

There is extensive empirical evidence that demonstrates that animals adjust food quality and alter their behaviour to reduce the risk of predation and increase their chance of survival (McNamara and Houston 1987). Similarly, female *E. macquarii* adjust nesting behaviour and reduce the amount of time spent on land in high predation risk areas to increase their chance of survival. How they assess potential predation risk is species specific. Avoidance of a predator odour can be species specific (Swihart 1991, Nolte *et al.* 1993, Downes and Shine 1998) or a general response to a carnivore (Stoddart 1982, Nolte et al. 1994). However, the preferences demonstrated in the island experiments cannot be explained as a generalised avoidance of predator odour, as female *E. macquarii* show little response to fox odour and probably detect foxes by visual recognition. Female turtles are extremely wary when they emerge to nest and return to water when disturbed. If foxes continually pass through the nesting area, female turtles may make several false nesting attempts before deciding on a nest site and female turtles may assess predation risk by the amount of predator activity and the number of nesting attempts. *Emydura macquarii* appear to use a higher level of predator detection in relation to native predators. Gravid females responded similarly to eastern quoll odour as they did in high fox predation risk areas, thus the same antipredatory response occurs to the threat of two different predators but using different mechanisms of detection. Many turtles may have never been exposed to predation pressures by quolls, thus this response is an innate behavioural shift to the presence of quoll odour, which may also represent a response to direct predation pressure by quolls. Very little is known about predation pressures by native predators prior European settlement, as most native predators have been displaced by foxes on the Murray River, but the behavioural shift in response to quoll odour is similar to the response to fox predation pressure, suggesting that native dasyurids may have harassed or destroyed nesting turtles, as many prey only respond to predators that are actively dangerous (Dickman 1992).

In conclusion, this study demonstrates that female turtles alter their nesting behaviour in response to direct predation risk and also demonstrates that some predator-prey co evolution is present in this system. I have demonstrated that reproductive success of *E. macquarii* is reduced in high predation risk areas, as turtles respond to the presence of foxes and respond innately to the odour of a native predator, by which turtles perceive risk and alter nesting behaviour to reduce the amount of time spent on land. Studies on nest site preferences in turtles have primarily concentrated on both microand macro- habitat variables, however factors such as perceived predation risk may ultimately drive nest site selection in turtles.

Chapter 8 Incubation and Synchronous Hatching

8.1 Introduction

Juvenile turtles usually emerge from a nest together, despite the high probability of different rates of development within single nests of turtles (Gyuris 1993). Development of embryonic turtles is more rapid at warmer than at cooler temperatures within the normal range of incubation temperatures (Thompson 1997) and the temperature of incubation in nature depends, in part, on the position of eggs within a nest (Maloney et al. 1990). Chelonian nest structure is consistent across many species, with eggs deposited in more than one layer in a flask-shaped, air-filled nest chamber (Packard et al. 1993). The vertical distance between the eggs at the top of the nest and those at the bottom results in different temperatures of incubation and hence different rates of development (Thompson 1988a). The influence of different rates of development on incubation period are inconsistent with neonates emerging from the nest as groups, unless hatchlings remain in the nest for a period of time or eggs within a clutch hatch synchronously regardless of development rate. In this paper I address this inconsistency by investigating mechanisms of hatching synchrony.

Synchronous hatching and group emergence of young turtles should have several selective advantages. For example, the survivorship of neonatal sea turtles is likely to be higher if more than ten attempt to dig to the surface at one time (Carr and Hirth 1961). Additionally, predation on young turtles is very high (Herman et al. 1995), so the emergence of many young turtles may swamp predators (Arnold and Wassersug 1978) because the emergence of more neonates decreases the chance of predation through the *per capita* dilution of individual predation risk (Dehn 1990). Indeed, synchrony in the timing of births has evolved as a predator-avoidance strategy in many species (O'Donoghue and Boutin 1995).

I used the Australian pleurodiran turtle, *Emydura macquarii*, as a model to investigate possible hatching synchrony in turtles because the effects of temperature on incubation period (Thompson 1997) and temperature differentials within natural nests (Thompson 1989) are well known. Eggs at the top of a nest of *E. macquarii* may be 6 °C warmer than the eggs at the bottom of the same nest, yet emergence of hatchlings is synchronous (Thompson 1989). Thus, I postulated that, for hatching to occur synchronously, 1. warmer, more advanced eggs must delay emergence or slow their developmental rate, or 2. cooler, less advanced eggs speed their rate of development or hatch at a developmentally earlier stage than their sibs. I refer to these two possibilities as the waiting and catch-up hypotheses,

respectively, and in nature, both mechanisms could operate. Possible advantages of synchronous hatching and group formation are also discussed.

8.2 Materials and Methods

8.2.1 Developmental Temperature and Hatching Synchrony

Female *Emydura macquarii* were captured in Lake Mulwala between 24th October and 8th November 1997 and turtles were held in large water-filled, holding drums in a protected shed, and fed twice a week with yabbies (*Cherax destructor*) and European carp (*Cyprinus carpio*). Water was cleaned within 24 hours after feeding. At the end of the trapping period, oviposition was induced, eggs were marked and transported to Sydney within 24 h of collection (chapter 2).

Twelve eggs were selected randomly from each clutch. Six eggs were placed in two rows, so that eggs were not in contact with each other, in two plastic containers (75mm x 200mm x 55mm). Eggs were incubated in vermiculite maintained at a constant water potential (chapter 2).

A total of 24 clutches and 288 eggs were used in two experimental and two control groups that contained six replicate clutches. For both experimental groups (Fig. 8.1a and 8.1b.) clutches were evenly divided into two separate containers. Each half clutch was either incubated at 25 °C or 30 °C for one

week to establish developmental asynchrony. After a week, the eggs that were held at 30 °C in the first experimental group were removed from their containers and placed next to the eggs from the same clutch that were held at 25 °C (Fig. 8.1a). The container was then re-weighed before being incubated at 25 °C until hatching. Conversely the eggs held at 25 °C in the second experimental group (Fig 8.1b) were removed from their containers and placed next to the eggs from the same clutch that was held at 30 °C, and the clutch was incubated at 30 °C until hatching.

The control groups (Fig. 8.2) were initially treated the same as the experimental groups, but the entire clutch was held at the same temperature (each half in separate containers) for the first week of incubation, either at 25 °C (control group one) or at 30 °C (control group two). The eggs from one of the containers were then placed next to the eggs from the same clutch in the other container and held at the same initial temperature (either 25 °C or 30 °C) until the end of the incubation period.



Fig. 8.1. Experimental design (a) Experimental group one; eggs from a single clutch were divided and incubated separately at either 25 °C or 30 °C for a week, and then held together at 25 °C until completion. (b) Experimental group two: a similar design to (a), however the clutch was held together at 30 °C until completion.

Chapter 8: Hatching Synchrony 154



(a) Control group two (control2)

Fig. 8.2. Experimental design (a) Control group one; eggs from a single clutch were divided and incubated separately at 25 °C for a week, and then held together at 25°C until completion. (b) Control group two: a similar design to (a), however the clutch initially incubated separately at 30 °C and then held together at 30 °C until completion.

From day 40 of the incubation period, containers were checked at 09:00 and 18:00 each day for hatchlings. The time of pipping (initial breaking of the egg shell by the hatchling), as well as the time of hatching were recorded, and emerged hatchlings were examined for an external yolk sac and then removed from the containers. For statistical analyses, the time until emergence from the egg constituted the incubation period.

There are three factors in this experimental design; initial incubation temperature (either 25 °C or 30 °C), movement of eggs (i.e. whether an egg was left in the same container or placed into a different container after the initial week of incubation) and developmental stage of the neighboring egg (i.e. different in development as in experimental groups or the same as in control groups. A general linear model was used to test whether movement affects incubation time, whether clutches in the experimental groups hatched synchronously, and the mechanisms of synchronous hatching (catch-up or waiting). I then analysed the response variables individually using independent paired t-tests.

For synchrony to occur, eggs within a clutch with different developmental stages should have similar incubation periods (experimental groups). The mechanism by which synchrony occurs (catching up or waiting), are revealed by comparing the incubation periods of eggs maintained at the same temperature throughout the experiments, but with eggs placed next to them of either different or the same developmental stage. The catch-up hypothesis predicts that, from experiment 1 (Fig. 8.1a), less developed eggs (at 25 °C) with advanced eggs (at 30 °C) placed next to them will hatch prematurely and have shorter incubation periods than all other eggs at 25 °C either moved or unmoved (Fig. 8.1a).

In contrast, the waiting hypothesis predicts that advanced eggs (incubated at 30 °C), from experimental group two, with less advanced eggs (25 °C) placed next to them (Fig. 8.1b) should hatch significantly later than all other eggs incubated at 30 °C. The experimental group would retard development or hatching until less advanced embryos reach hatching stage.

Emydura macquarii embryos do not compensate for changes in incubation temperature (Booth 1998b), thus embryos with altered temperature regimes in the experimental groups will have different incubation periods to their sibs (incubated at a constant temperature) if they were incubated separately. Also, sex determination in *E. macquarii* is not temperature dependent (TSD) but genetically determined (Thompson 1988b), thereby excluding differential incubation periods between hot and cold temperature regimes due to sex effects.

8.2.2 Group Size, Nest Emergence and Predation Risk

A further 88 eggs collected in October 1998 were held at 30 °C for the duration of incubation. In January 1998, the hatchlings from all clutches were randomly allocated into two group sizes of either 1 or 10 animals, and placed in previously excavated turtle nests, between 10 m and 20 m from the water located around two lagoons near Albury, NSW. At each lagoon, two groups of ten turtles were placed in nests during the day and two groups were placed in nests at night when different predators are active. Similarly, two individuals were placed in separate nests around each lagoon during the day, as well as two individuals at night. Hatchlings were buried with surrounding soil to simulate an actual nest of recently hatched turtles. Each nest was observed by a single person, camouflaged in a canvas sack, from 50 m away during the day using binoculars (Tasco 10x21) and 20 m away at night with a night vision monocular (Starlazer). Time until emergence, hatchling survival and predator types were recorded. An χ^2 was used to test for the treatment effects of group size on individual survival.

8.3 Results

8.3.1 Hatching Synchrony and Developmental Temperature Main treatment effects of initial temperature, movement of the eggs and treatment group and each interaction terms were highly significant (Table 8.1). Moved and unmoved eggs within control groups did not differ in their

incubation periods suggesting movement alone did not influence hatching times. To test for synchrony and its causes, I was concerned with the interactions of particular treatments and not the main effects *per se*, on incubation times. For synchrony to occur I tested the hypotheses that the incubation period of eggs in the first and second experimental groups were not significantly different.

Ha: unmoved/25 °C/exp1 = moved/30 °C/exp1 (A v B Fig. 8.1)

 H_a : unmoved/30°C/exp2 = moved/25°C/exp2 (C v D Fig. 8.1)

| | Degrees of freedom | F-value | p- value |
|--|-----------------------|---------|----------|
| Treatment (Experimental and Control) | 1 | 143 | P<0.001 |
| Movement | 1 | 14 | P<0.001 |
| Initial Temperature | 1 | 2162 | P<0.001 |
| Treatment x Movement | 1 | 19 | P<0.001 |
| Treatment x Initial Temperature | 1 | 1454 | P<0.001 |
| Movement x Initial Temperature | 1 | 938 | P<0.001 |
| Treatment x Movement x Initial Temperature | 1 | 984 | P<0.001 |
| Error | 40 | | |

Table 8.1. Table of results from the general linear model.

Paired t-tests showed that synchronous hatching occurred in the second

experimental group (Fig 8.1b) where less developed eggs were moved next to

advanced eggs and development proceeded at 30 $^{\circ}$ C (t₅ = 0.72 p =0.50).

However, advanced eggs moved next to less advanced eggs at 25 °C, hatched

significantly earlier than their less advanced sibs in the same nest ($t_5 = 8.86 \text{ p} < 0.001 \text{ Fig. 8.3a}$).

Nevertheless, there were indications that synchronous hatching may occur as predicted by the catch-up hypothesis.

Ha: unmoved/25 °C/exp1 < unmoved/25 °C/control1 (A v E Fig. 8.1 and 8.2)

Eggs incubated at 25 °C with advanced sibs next to them (experimental group one) hatched up to 5 days earlier than eggs kept at 25 °C with sibs of the same development next to them (control group one) ($t_5 = 4.99 \text{ p} < 0.001 \text{ Fig 8.3a}$). In contrast, predictions from waiting hypothesis were not supported; the incubation periods of eggs at 30 °C with less advanced sibs (from the second experimental group) were not significantly different from eggs at 30 °C with sibs of the same development history ($t_5 = 1.14 \text{ p} = 0.28 \text{ Fig. 8.3b}$). These results suggest that there is no delay in time of hatching in the presence of less developed eggs.

8.3.2 Group Size, Nest Emergence and Predation Risk

Hatchlings in groups emerged from the nest on average 13 minutes earlier than individuals ($F_{1,15}$ = 15.0921 p=0.002), and on all occasions at least seven hatchlings emerged from the nest within 30 seconds of the first hatchling to emerge. No predation on hatchlings occurred at night. During the day, group size significantly affected individual predation risk (χ^2 = 4.94 p=0.026 df =1); two of the four (50%) individual hatchlings released from a nest were killed, compared to only four of the forty (10%) hatchlings released as a group. The Australian magpie (*Gymnorhina tibicen*) was the only predator.

8.4 Discussion

During the manipulations of embryonic developmental stages within a nest, hatching synchrony occurred only in nests where less advanced eggs were moved to the higher temperature and next to more advanced sibs. Nevertheless, the presence of more advanced embryos (initially incubated at 30°C), appeared to stimulate the less advanced eggs (in experimental group 1) to hatch earlier than the eggs at the same stage in the control groups (Fig. 3a), suggesting they were catching-up to their more advanced sibs. Failure to hatch synchronously may have occurred because the temperature regimes meant these less advanced eggs were still too premature to hatch when the advanced eggs hatched despite the stimulus to hatch early from the hatching of advanced eggs. Nevertheless, that they hatched significantly earlier than the controls suggests that their development may have been accelerated by the presence of advanced eggs earlier in incubation. Similarly, eggs of bobwhite quail (Colinus virginianus) hatch early when placed next to more advanced eggs, but the more advanced quail eggs are also held back by the least developed eggs (Vince 1968). However, I found no evidence of embryos



(a) Incubation period of Control group one and Experimental



Fig. 8.3. (a) Incubation periods of eggs in control and experimental group one. Synchronous hatching did not occur, however less advanced eggs hatched significantly earlier than its control, supporting the 'catchup' hypothesis. (b) Incubation periods of eggs in control and experimental group two. Synchronous hatching occurred in experimental group two but the more advanced eggs were not delaying hatching, thus rejecting the 'waiting' hypothesis.

Catchup

delaying hatching (waiting hypothesis) as more advanced eggs with less developed eggs placed next to them did not hatch earlier than the control group eggs.

Neonatal reptiles that hatch early often have incompletely internalised yolk sacs (Packard and Packard 1988). Surprisingly, there were no differences in the number of hatchlings with external yolk sacs in any of the experimental groups. Thus, despite the imposition of shorter incubation periods, embryonic development seems to have been accelerated rather than neonates hatching prematurely. Under-developed hatchlings that emerge early may be disadvantaged, in terms of agility and performance, compared to the more developed turtles, and hence any benefits of group emergence could be outweighed. For example, Japanese quail chicks (Coturnix coturnix japonica) with accelerated development stand one-two hours later than normal chicks (Vince and Chinn 1971). If the nervous system of early hatching turtle embryos is similarly less developed than full-term hatchlings, their relative co-ordination and fitness compared to the full-term embryos may be reduced and the risk of predation to both land and aquatic predators could be greater. Thus, there may be a trade-off between the advantages of synchronous hatching and possible disadvantages of premature hatching in some eggs, which warrants further investigation.

It is possible, however, that the less advanced embryos hatched prematurely without trading off development. Oxygen consumption of embryonic *E. macquarii* increases to a peak during development followed by a decline of up to 25% from peak consumption (Thompson 1989). A similar pattern of oxygen consumption occurs in ratite birds where embryonic growth is essentially complete at the peak of oxygen consumption, several days before hatching (Vleck et al. 1979). The less advanced embryos within a clutch shorten or eliminate the phase of development after the metabolic peak and hatch at the same time as more advanced embryos without trading off development (Vleck et al. 1979). Regardless of whether there are disadvantages to early hatching by some eggs in a clutch, the occurrence of hatching synchrony in clutches of *E. macquarii* suggests that there is some advantage.

The origin for such behaviour is difficult to determine, however pressure from predation can alter the timing of reproductive events such as birth (O'Donoghue and Boutin 1995). Emergence from the nest as a large group could swamp and confuse predators or simply dilute an individual's risk of predation amongst other members of the group. Hatchling sea turtles (*Caretta caretta*) exhibit a novel terrestrial locomotor behaviour, the hatchling frenzy, characterised by rapid movement from nest to surf (Dial 1987). The hatchling frenzy in *C. caretta* may have evolved to reduce their exposure time to predators while on the beach or confuse potential predators. Conversely, a large group of turtles emerging from a nest could attract predators that would have otherwise been unaware of nest had hatchlings emerged individually.

I found that hatchlings in groups emerge from the nests much quicker than individuals, and preliminary results suggests that hatchlings in groups also have a reduced risk of predation to common avian predators. Six Australian magpies (*Gymnorhina tibicen*) attacked hatchlings emerging from nests and each bird had difficulty swallowing hatchlings. Most birds could only process one turtle before the remaining members of the group completed the journey to the lagoon, hence hatchlings may have a small degree of defense to common avian predators, at least until other turtles from the nest have reached the water. Similarly Large-mouth Bass (*Micropterus salmoides*) reject red-eared sliders (*Trachemys scripta*) and painted turtles (*Chrysemys picta*) because the hatchlings claw and bite the gill apparati or digestive tract of Bass (Britson and Gutzke 1993).

Synchronous hatching facilitates quicker group emergence from the nest, which in turn can reduce the predation risk of an individual via the dilution effect (Dehn 1990). Emerging as a group can offset any disadvantages, such as reduced agility that a hatchling may incur by hatching early. Predation risk may not be diluted evenly amongst the group as, compared to the more advanced hatchlings, the increased predation risk due to reduced agility and a greater time spent on land by early hatchlings could be real. However, the likelihood of a fellow group member hatching at an earlier stage is great, and if a predator, such as the magpie, can handle only one hatchling per group, emerging from the nest with both stronger and weaker individuals will still reduce predation risk compared to emerging individually.

Emydura macquarii eggs are usually laid into a clay or soil base that becomes dense and compacted throughout the incubation period and successful emergence from the nest by Hawksbill sea turtles (*Eretmochelys imbricata*) decreases with increasing soil compaction (Horrocks and Scott 1991). Synchronous hatching may facilitate quicker emergence from the nest as hatchlings in groups emerged from the nests significantly earlier than individuals. The selective advantages of behavioural traits are difficult to determine, as both the cause and effect of a particular trait can be mutually exclusive. For example, it is possible that synchronous hatching may have evolved to facilitate quicker emergence because hatchlings in groups emerged from the nests significantly earlier than individuals, but it may also dilute an individual's predation risk to avian predators, and vice-versa.

Synchronous hatching of common rhea (*Rhea americana*) eggs occurs when later-laid eggs are in contact with earlier-laid eggs throughout the incubation period and some event late in incubation, possibly acoustic signals between eggs, allows early hatching of later-laid eggs (Faust 1960). However, there are no reports of vocalisation in turtles and the eggs in this study were not in contact with each other, but the auditory sounds from physically pipping the shell may stimulate synchronous hatching. Very little is known about the stimuli of synchronous hatching, but the decelerating embryonic metabolic rate late in development may signal to less advanced eggs, through a combination of changes in oxygen consumption, carbon dioxide production, and heart rate, that hatching is imminent. Three patterns of acceleration of the heart rate are unique to the external pipping period of avian embryos: irregular intermittent large accelerations, short-term repeated large accelerations and relatively long-lasting cyclic small accelerations (Tazawa et al. 1999). Mean heart rate during pipping is also maximal for many birds and is usually higher than that of hatchlings (Pearson and Tazawa 1999) and perhaps the early turtle embryos are stimulated to hatch because of fluctuating or increasing heart rates of turtles beginning to pip their egg shell. However, the mechanisms of synchronous and asynchronous hatching are far from resolved and much further research is required.

My data strongly support the catchup hypothesis, whereby less advanced embryos either increase their developmental rate or hatch significantly earlier than normal in the presence of more advanced eggs, and also support the hypotheses that *E. macquarii* hatchlings emerge from nests quicker in groups. Synchronous hatching facilitates group emergence, which may reduce individual predation by the 'dilution' effect.

Chapter 9 General Discussion

9.1 Key Findings

Several major conclusions stem from my study of the population, community and reproductive ecology of *E. macquarii* in the Murray River:

(i) *Emydura macquarii* prefers lagoons to the mainstream in the upper Murray River, possibly relating to resource availability and reduced water temperatures from the release of water from dams and impoundments.

(ii) *Emydura macquarii* delays maturity and produces one relatively large clutch of eggs (~21 eggs) annually. The von Bertalanffy model describes the growth of both female and male turtles, which mature at 10-12 years and 5-6 years respectively. Growth is rapid over the first few years, declines close to maturity, and is indeterminate beyond maturity. Clutch size is positively correlated with body size, but annual variation in clutch size is partly attributed to environmental conditions prior to oviposition.

(iii) *Emydura macquarii* has a Type III survivorship curve, where survival is related to age. Most mortality occurs in the egg and hatchling stage, and
survival of adult turtles is over 95% each year. Foxes kill a small proportion of the nesting female population annually.

(iv) Populations of *E. macquarii* in the upper Murray River may be declining from predation pressure by foxes. Population stability relies predominantly on survival of adults, which make up the majority of the populations.

(v) Predation on nests by the introduced red fox is extremely high, with over 90% of nests destroyed annually. Nests laid in sand, rather than grass, away from trees and the banks of lagoons have a much better chance of avoiding predation, although foxes are able to detect turtle nests by slight disturbances of the ground, as well as olfactory cues, anywhere.

(vi) Reproductive success is reduced by sub-lethal impacts of predation because turtles modify their nesting behaviour in high predation risk areas. Some predator-prey co evolution occurs in this system because turtles respond innately to chemical cues of native predators. *Emydura macquarii* eggs hatch synchronously by either increasing their developmental rate or hatching prematurely. Group emergence reduces time spent in the nest and predation risk through the 'dilution' effect.

9.2 Life History and Predation

The role that predation plays in influencing life history traits has been explored in many animals (see Andrewartha and Birch 1984), yet few studies have focused on the affect of predation on various life stages and the life history of vertebrates. Nest predation rates are over 90% along the Murray River, but almost all embryos in the small proportion of nests that avoid predation will complete the incubation period and emerge from the nest (chapter 6). Prey species have two fundamental strategies for reducing their probability of being killed by a predator: behavioural modification and morphological defences (Abrahams 1995). The risk of predation may have modified the timing of hatching and nest emergence of hatchling turtles. Synchronous hatching of *E. macquarii* may be a direct response to predation pressures on hatchlings emerging from the nest (chapter 8). Eggs less developed increase their rate of development or hatch early to facilitate group emergence from the nest, which reduces predation risk between the nest and water but may trade-off fitness by hatching early. Anti-predatory defences and fitness trade-offs of eggs and hatchlings occur in other animals. Arboreal eggs of red-eyed tree frogs (Agalychnis callidryas) hatch early if attacked by predators and if left undisturbed, tadpoles are less likely to be taken by aquatic predators upon entry into the water because they hatch at a later developmental stage (Warkentin 1995, Warkentin 1999).

Hatchling *E. macquarii* that emerge from the nest and enter the water suffer high mortality rates, possibly due to size-related predation pressures (chapter 6). Juvenile painted turtles (Chysemys picta) bask for significantly shorter periods than adults, due to a higher risk of predation (Lefevre and Brooks 1995). Growth of *E. macquarii* is extremely rapid over the first few years but declines close to maturity (chapter 4) and over the same period, survival rates increase from 10% to 70% by the late juvenile stage, a pattern of growth and survival similar to *Kinosternum flavescens*, where survival is over 90% by maturity (Iverson 1991a). Selection often favours individuals that grow rapidly when size-related predation is intense. Mortality due to predation is extremely high in young Yellow Perch (Perca flavescens), but individuals that grow faster have a much better chance of survival than slower growing individuals (Post and Prankevicius 1987). Similarly, intense predation on young water snakes (Nerodia sp.) that have little defence against predatory birds, selects for individuals that are difficult to detect and that grow rapidly (Mushinsky and Miller 1993).

Female turtles in higher latitudes may delay maturity and produce a relatively large clutch of eggs because they are constrained by the number of clutches that can successfully incubate each year (St Claire *et al.* 1994). In many other animals, differences in age at maturity among populations are phenotypic responses or adaptations to the presence of predators, and predation and mortality play a significant role in interpopulation differences in life histories. Guppies in high predation environments mature earlier and reproduce more often than those in low predation environments (Reznick 1996). Yet, when placed in areas of low predation, guppies originally from areas of high predation also delay maturity (Reznick 1996). As E. macquarii grows, mortality rates and thus, predation risks become extremely low. Consequently, female sexual maturity is delayed, which increases reproductive output. Female *E. macquarii* mature around 10 years of age and produce a large clutch of eggs, thereby maximising reproductive potential, as clutch size is positively related to body size (chapter 4). Most females produce only one relatively large clutch of eggs per year (~21 eggs), but the number of eggs produced can vary depending on environmental conditions. If winter and spring rainfall is below average and temperatures are above average, female turtles may produce a smaller clutch of larger eggs, thus improving the fitness and survivorship of hatchlings that incubate in potentially hot and dry conditions (chapter 4).

Predation and mortality rates of nests of *E. macquarii* may have increased since foxes were introduced to Australia in the 1870s (Saunders *et al.* 1995). Prey species that possess morphological defences, such as the carapace and plastron of a turtle, should exhibit less behavioural modification in response to predation risk than species lacking such defences (Abrahams 1995). One problem is that current traits reflect former conditions (Congdon and Gibbons 1990) and the armour of *E. macquarii* may not be effective against foxes. Foxes detect nests using both olfactory cues of eggs and slight soil disturbances, which lead to increases in nest predation in exposed areas (chapter 7), but female nesting behaviour may also have been modified. Nest site selection is influenced by predation risk in many animals, such as Arctic loons (Gavia *arctica pacifica*), where foxes, gulls and voles prey on nests, and the selection of nest sites is an adaptive response to varying annual selective pressures by their predators (Peterson 1979). To reduce their risks of predation, female E. *macquarii* nest close to the water, thus reducing potential nesting areas where hydric and thermal incubation conditions greatly increase the fitness of her offspring (McGehee 1990, Bobyn and Brooks 1994a Bobyn and Brooks 1994b, Janzen 1995, Elphick and Shine 1998). Hatchling performance is influenced by the hydric conditions of the incubation substrate in *Chelydra serpentina* (Miller 1993) and thermal conditions can reduce survival of many species of turtle (Wilson 1998, Weisrock and Janzen 1999). Predation is a significant source of mortality in *E. macquarii*, as it was prior to European settlement and the introduction of foxes, because some co evolution between native cats and turtles exists. Turtles avoid areas where the chemical cues of Eastern quolls are present, which were potential predators of turtles and their nests.

9.3 Management Strategies

Foxes are having an impact on populations of *E. macquarii* in both the upper and lower Murray (chapter 6, Thompson 1983b). Predation on nesting female *E. macquarii* has not been reported before and, along with high nest predation rates, upper Murray River populations are declining at almost 5% per year. Few management plans have ever been designed to preserve freshwater turtles, primarily because little is known about their life history and factors affecting their survival. Among Australian turtles, only the western swamp turtle (*Pseudemydura umbrina*) in Western Australia is currently listed as endangered, although *E. macquarii* subsp. in the Bellinger River catchment is listed as vulnerable (Appendix 1). Western swamp turtle numbers were as low as 20-30 individuals until management plans were implemented in 1987 (Burbidge and Kuchling 1994, Cann 1998). Eggs were collected for headstarting programs and electrified fox-proof fencing was erected around the main swamps they inhabit, and there are presently over 150 turtles in the population (Cann 1998).

Erecting fox-proof fencing to protect *E. macquarii* in the Murray River is not currently feasible, but management options that concentrate on reducing adult mortality by foxes would be far more beneficial to population stability than any other strategy (chapter 6). Headstarting programs, alone, are unlikely to have a major influence on maintaining population numbers. The biological benefits of headstarting programs are overestimated for sea turtles; when subadult and adult survival is reduced, headstarting cannot compensate for losses in later stages (Heppell *et al.* 1996b). Eliminating foxes completely from the southeastern Australia to reduce nesting female mortality is currently not an option for *E. macquarii*, although strategic fox reduction around important habitat is feasible. The majority of female turtles emerge to nest in November. Reduction of foxes by baiting and shooting (chapter 5) prior to nesting would reduce adult mortality and stabilise the population (chapter 6). New foxes will move into the free territories relatively quickly (Thompson 1994), but not before turtle nesting is complete. The relatively simple and inexpensive option of using turtle excluder devices on trawl netting has reduced the incidence of sea turtle strandings (Crouse *et al.* 1987) and removal of foxes on the Murray River, prior to nesting, should provide similar results.

Key habitat must also be identified. In the upper Murray, the majority of *E. macquarii* inhabit permanent lagoons and it is these areas where management should be directed. Lagoons that are connected to the River during small floods, such as Cook's lagoon, are high priority areas, as they would promote dispersal of turtles to other areas under high predation pressures. The hypothesis that islands in Lake Mulwala may be important nesting areas because they are fox free has merit (Thompsons 1993). Currently, foxes swim to the islands from the mainland, but if their numbers were kept in check through baiting, the islands could become important hatching and recruitment grounds. Turtles travel large distances in these Lakes, often moving many kilometres upstream (unpubl. data), so the islands could become recruitment grounds for most upstream populations. These management strategies are relatively less intense and costly than my fox removal study, and they provide options that can be applied over a wide temporal and spatial scale. They can also co-exist with current agricultural practices in southern Australia, where wide-scale fox baiting occurs from June-October to reduce predation on lambs (Saunders *et al.* 1995).

Successful management depends on regular flooding to permit the dispersal of both juvenile and adult turtles. Dams are insufficient to prevent major floods in the Murray but have decreased the frequency of minor floods (Smith and Smith 1990). Many lagoons have remnant connections to the mainstream and perhaps regular increases of the River water level will be enough to connect them and permit dispersal. In theory, this management strategy should have the dual effect of maintaining adult turtle numbers but also increase the proportion of juveniles in the population, thus reducing the elasticity value of adult turtles (chapter 6). In practice, its success may be limited in the upper Murray, where water temperatures of the mainstream are low (chapter 3). Because water from Hume Weir is released from the bottom of the dam, the water temperatures between Albury and Mulwala are much cooler than further downstream (Shafron et al. 1990), making it uninhabitable for large densities of turtles. Below Lake Mulwala, E. macquarii are regularly caught in the mainstream, as well as backwaters and lagoons (Chessman 1988b).

The control of foxes in my removal experiment applied methods used by many management agencies in Australia to control foxes in rural and semirural areas. These results can be interpreted in terms of both costs and benefits of fox control. The benefits are reduction in predation pressures on turtle populations and an increase in lambing success (Saunders et al. 1995), but the costs include the financial costs of laying baits, and the ecological consequence of removing foxes. The ecological costs of fox control are increasing rabbit and hare densities (Banks 1997) that could have a significant impact on vegetation and other fauna. However, the wide scale management options would have limited impact on foxes (only during the turtle nesting and lambing periods) for most of the year and ultimately there should be little long-term change to rabbit numbers. The benefits of this management strategy may also apply to both *C. longicollis* and *C. expansa* which nest in similar habitat to *E. macquarii* and predation on their nests are likely to be at similar rates to *E. macquarii*. However, applying general management strategies to other species and even the same species in different geographic regions should be done with caution, as the life history of each turtle could be very different from *E. macquarii* on the Murray.

The life history of freshwater turtle populations are not complex and can usually be divided into three or four distinct life stages: eggs and hatchlings that usually spend a period of time incubating or traversing land; a juvenile stage that is primarily aquatic; and an adult stage that is aquatic but spends time on land to oviposit. Baseline demographic data evaluating growth and survivorship schedules of these various stages are central to developing effective management strategies. *Emydura macquarii* is a relatively slow growing and late maturing species that has high early mortality and adult survival, and management strategies that control adult mortality is more effective than any other strategy (chapter 6). The most cost effective and easily manipulated stage to eliminate predation by foxes is the period of time that female *E. macquarii* emerge to nest. Each species and population must be assessed independently, but currently *E. macquarii* populations on the Murray are under serious risk of decline because of predation by the introduced Red fox (*Vulpes vulpes*).

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