ECOLOGY OF THE EASTERN LONG-NECKED TURTLE (*CHELODINA LONGICOLLIS*) ALONG A NATURAL-URBAN GRADIENT, ACT, AUSTRALIA

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A thesis in fulfilment of the requirements for the degree of

Doctor of Philosophy

Institute for Applied Ecology

University of Canberra

January 2015

Certificate of Authorship of Thesis

Except where clearly acknowledged in footnotes, quotations and the bibliography, I certify that I am the sole author of the thesis submitted today entitled –

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Statement of Contribution

The thesis entitled *Ecology of the eastern long-necked turtle (Chelodina longicollis) along a natural-urban gradient, ACT, Australia* includes a published manuscript (Chapter two), a manuscript in review (Chapter three), and two manuscripts prepared for publication (Chapter four and five), which were written under the supervision of my thesis supervisors Prof. Arthur Georges (Institute for Applied Ecology, University of Canberra) and Assist. Prof. John H. Roe (Department of Biology, University of North Carolina).

These people provided guidance throughout the conception, analysis, writing and scope of these chapters, and they are included as authors in the associated publications. I have not received other assistance than stated above.

As chair of the supervisory panel I agree with the above statement.

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Prof. Arthur Georges

Date: …………………………………….

Acknowledgements

It has been a very nice journey in the last few years while moving to Australia and doing my PhD, with a lot of personal and professional learning, and achievements.

First I would like to thank some key people that helped me to initiate contact with my supervisors and made possible the connections to study in Australia. I acknowledge Valentine Lance who initially put me in contact with Arthur Georges and Carla Eisemberg who helped to strengthen this collaboration.

I am very grateful to my supervisor Arthur Georges in accepting me as his student and taking my supervisor John Roe on board in this project. Both of you were instrumental in establishing this research and giving me advice and support through my candidature. It's has been a real honour to work with you both, and I am glad I continued my studies with turtles through the PhD and we could share mutual interests in chelonian research.

While in Canberra, I had support from several people. I would like to thank the Institute for Applied Ecology (IAE) team: Vicky Smith, Barbara Harriss, Karen Mow, Jayne Lawrence, Jane Ebner, and the late David Choquenot for making the life of students easier in relation to administrative and day-to-day matters; the Animal House team: Jacqui Richardson, Alistair Zealey and Wendy Ruscoe for helping keeping turtles for x-ray; and the IAE students Carla Eisemberg, Maria Boyle, David Wong, Larissa Schneider, Veronika Vysna, Kate Hodges, Debora Bower, Stuart Pittard, Chamani Marasinghe Wadige, Teresa Gonzales, Elodie Modave, Rheyda Hinlo, Alan Couch, Wayne Hart, Margarita Medina, Paul Sutherland, Rakhi Palit, Matthew Young, Maria Angelica Lopez, Scott Thomson, and Sherri Lehman for their support and companionship. Some people provided their time and expertise on some topics related with this thesis: Sharon Kazemi,

Graeme Hirth, and Carlos Gonzalez-Orozco (ArcMap); Angelica Lopez-Aldana, Julio Romero, and Maria Boyle (stats); Bernd Gruber (MARK program); Evan Harrison, Fiona Dyer, and Ross Thompson (Freshwater lab); Bill Maher, Frank Krikowa, and Veronika Vysna (Ecochemistry lab); Rifaat Shoukrallah (Territory and Municipal Services). I also would like to thank everyone who volunteered to help in my field work, including Shirley Famelli from Brazil, and friends outside the university: Taylor Yoon and family, Ruben Ramirez (El negrito), Alessandro Guilhon, and Edwin Castilho.

I would like to acknowledge the support from people from other institutions that were essential for this project: Shane Dawson and Wade (Gungahlin Lakes Golf Club), Phil Dumbar (Ginninderra Experimental Station), and the rangers Peter Mills, Grant Woodbrigde, and John Lawler (Mulligans Flat Nature Reserve).

A special thanks to my family back in Brazil (pai, mãe, Gui e Pati), and my wife and kids (Giselle, Sofia e Caetano), all your support, friendship and being always there was essential to complete my studies and make life happier.

While doing my PhD, I was supported by a national Endeavour International Postgraduate Research Scholarship and a University of Canberra W.J. Weeden Scholarship, and this project was funded by the Institute for Applied Ecology, the ACT Herpetological Association and Turtles Australia Inc. This research was conducted with the appropriate approvals and permits from the University of Canberra Committee for Ethics in Animal Experimentation and Environment ACT.

Abstract

Urbanization is one of the leading causes of biodiversity loss worldwide. Many species living within natural-urban gradients are in contact with urban stressors and ecological studies are needed to understand biological responses of susceptible species. Semi-aquatic reptiles engaging dispersal and large distance movements within the city can be susceptible to road mortalities and predation. Freshwater turtles are no exception, as females engage in movements for nesting, males move large distance during the breeding season to search for mating opportunities, and both sexes can disperse to reach different ponds in response to prey availability and wet-dry cycles. In Australia, the eastern long-necked turtle (*Chelodina longicollis*) is a common species inhabiting a range of bodies of water, including suburban wetlands. Previous studies in a suburban area and an adjacent natural reserve during drought in the Australian Capital Territory demonstrated that the *C. longicollis* suburban population was more abundant, grew faster, moved longer distances, and did not exhibit aestivation behavior compared to their nature reserve counterparts, while both populations exhibited similar survivorship. This previous study also demonstrated that the movement dynamics of this species was influenced by wet-dry cycles. When the nature reserve ponds dried, the suburban ponds maintained water levels, and attracted turtles from the nearby reserve. After five years, many conditions had changed at the study site, including an increase in rainfall compared to the previous study, in addition to an increase in urbanization and associated infrastructure. A predator-proof fence was constructed around the nature reserve to protect against encroaching suburban hazards and feral predators. These changes created a unique opportunity to study the response of this turtle over time to an increase in suburban stressors in addition to climatic conditions. I considered three areas with different levels of suburban stress to evaluate *C.*

longicollis responses – a nature reserve with a low anthropogenic impact isolated by the enclosure fence, a rural site with an intermediate anthropogenic impact, including agriculture, low level of urban development and exposure to feral predators, and an suburban site with a high anthropogenic impact, including urbanization and exposure to feral predators. The goal of the thesis was to investigate responses of the turtles to dramatic habitat change brought about by urbanization, under a wetter climatic regime than occurred in earlier studies. Specifically, the objectives of this investigation was to evaluate the effects of a predator-proof fence on a reptile community and determine if there is a species-specific impact and the magnitude of the impact at the population level; to evaluate the spatial ecology and survivorship of female *C. longicollis* within the suburban area compared to females inside of the fence enclosure in the nature reserve, with the use of radio-telemetry; to investigate demographic responses, fecundity and vital rates of *C. longicollis* through a capture-mark-recapture study; and to evaluate the nesting ecology of *C. longicollis* in order to document incubation period and nesting success in natural nests, and investigate the possibility of overwintering in the nest by hatchlings.

I registered 1052 records of six species of reptiles along the predator-proof fence, but impacts, including number of records and mortality, were larger for *C. longicollis* than lizards and a snake species (Chapter two). I observed several *C. longicollis* recaptures at the fence and many were found dead later at the fence, indicating a persistent attempt to navigate past the fence. I conservatively estimated that the fence resulted in the death of 3.3% and disrupted movements of 20.9% of the turtle population within the enclosure. The most common cause of turtle mortality was overheating, especially on turtles trying to enter the reserve, followed by predation, vehicular collision and entanglement.

Considering the spatial ecology attributes, suburban and nature reserve female *C. longicollis* had similar movements and spatial metrics, except for suburban turtles moving longer total distances (Chapter three). There was no observation of prolonged terrestrial aestivation in any of the study sites. Turtles from smaller ponds used more wetlands than turtles from larger ponds, exposing them to increased risks from vehicular mortality during overland movements, a fact that was observed in the suburban site, as they showed reduced annual survivorship estimates (0.67), according to known fate models, compared to the nature reserve turtles (1.00) owing to the high number of vehicular collisions in the sample.

The capture-mark-recapture study revealed that turtles from the three study sites with different levels of anthropogenic impact had similar growth rates, abundances, sex ratios, and fecundity (Chapter four). Despite increasing urbanization, there was evidence of recent recruitment at all sites and survivorship estimates were similar among study areas, according to Cormack-Jolly-Seber models. In addition, some of the turtles were recaptured over long distances (6 km) from their initial encounter, underscoring the importance of movements in suburban landscapes. These findings contrast with the previous study during drought where nature reserve turtles grew slower, were less active and less vagile than suburban turtles owing to the fluctuating resources and water levels in the nature reserve compared to the more stable environment in the suburbs.

I was also able to confirm that *C. longicollis* hatchlings overwinter in the nest, spending on average 320 days from the date eggs were laid until emergence (Chapter five). In addition, I also observed two strategies from the same population, with hatchlings from one nest emerging in autumn and spending their first winter in the aquatic environment, and hatchlings from three nests overwintering in the nest and emerging in spring.

Together, these findings indicate that *C. longicollis* is a resilient species within suburban landscapes and its demography and behavior in strongly influenced by rainfall. The observations of turtles trying to migrate back to the nature reserve following flooding of ephemeral ponds in the reserve, in addition to the long distance movements and the fact that the current design of the fence did not allow turtles to reach the reserve ponds underscore the importance of allowing turtles to freely move between habitats in response to stochastic events such as drought. Even though the nature reserve turtles are now protected against nest predation by foxes inside the enclosure, the fact that the fence caused adult mortalities and did not allow immigrations suggests the population inside of the fenced enclosure would likely decline over the long-term if no action is taken. I suggest the construction of water under-passages along hotspots of turtle movements, which were clustered in areas with more wetlands and less urban development. The efficacy of this mitigation measure should be tested and a longer-term monitoring of the turtle population inside of the fence enclosure and within the suburbs should be encouraged to understand population responses over longer periods of time (i.e., decades), which are more reflective of turtle life spans. In conclusion, this work helps to demonstrate how the population dynamics of a nominally aquatic turtle is influenced by and regulated in space and time by populations from a range of habitats differing in anthropogenic impact. The remarkable capacity for overland movements in *C. longicollis* is what connects such unique and sometimes distant populations, and possibly helps in the persistence of this species in challenging environments.

Table of Contents

List of Figures

List of Tables

Page

General Introduction

Urbanization and wildlife

Urbanization is one of the most disruptive forms of habitat alteration, usually leading to a complete restructuring of vegetation and species composition, and causing local extinctions of many native species (McKinney 2002, 2008; Miller and Hobbs 2002; Shochat *et al.* 2006). During urban development, some managers try to maintain patches of the predevelopment vegetation, but these patches usually become more vulnerable to eventual colonization by non-native invasive plants and other degrading influences, such as predatory animals including dogs and cats (Luken 1997). Urbanization causes population declines in many groups of vertebrates, invertebrates, and plants (McKinney 2008). Usually, urban environments show a pattern of reduced native species richness and an increase in abundance for urban-tolerant species (McKinney 2002, 2006, 2008; Holway and Suarez 2006; Hamer and McDonnell 2008). On the other hand, low to moderate levels of human development, as usually observed in suburbia, are known to increase native species richness in mammals, birds, butterflies, bees, ants, lizards and plants, owing to increased environmental heterogeneity, in addition to the increased productivity from human augmented resources (McKinnney 2002).

Human population and urbanization rates are expected to increase in the next decades, especially in developing countries (World Resources Institute *et al.* 1996; Gakenheimer 1999; Schafer and Victor 2000). Consequently there is a need to understand the ecology of animal species susceptible to urban stressors to manage and mitigate possible impacts, if biodiversity in suburbs is to be maintained (Grimm *et al.* 2000, Ditchkoff *et al.* 2006). Some of the great challenges for urban wildlife are roads, which increase mortality risk, serve as a barrier to animal movement, affect home-ranges and migrations, and alter patterns of gene flow that can lead to genetic isolation (Adams and Geis 1983; Riley *et al.* 2006; Taylor and Goldingay 2010). Other threats faced by urban wildlife are habitat loss, pollution of water, soil and air, competition/predation by exotic species and interactions with humans and pets (Pickett *et al.* 2001; Parris and Hazell 2005). Maintenance of connectivity among patches of habitat and the use of underpasses and overpasses within urbanized landscapes are strategies that can facilitate movements, reduce mortalities and increase the chance of persistence of wildlife in such challenging environments (Bond and Jones 2008; Huber *et al.* 2012; Cushman *et al.* 2013).

Although some long-term studies have been conducted to understand the responses of wildlife to habitat alteration and urban stressors over longer periods of time (Petranka *et al.* 2003; Faeth *et al.* 2005; Fattorini 2011), there is still a lack of information on other factors that interact with urbanization, such as climate (Shochat *et al.* 2004). For example, as rainfall patterns can influence behavior, demography and ecology of vertebrates in natural habitats (Dickman *et al.* 1999; Lima *et al.* 1999; Madsen and Shine 2000; Greenville *et al.* 2013), we require greater understanding of the effects of rainfall patterns on life history of animals living in the border of suburban and natural habitats (Shochat *et al.* 2004; Parris and Hazell 2005) if we are to manage them to achieve best conservation outcomes. Further investigation is needed to understand how such factors interact in an increasingly urbanized world.

Freshwater turtles and urban challenges

Many freshwater turtle species inhabit urban waterways worldwide as a consequence of encroachment on their habitats, in addition to pet turtles release in urban waterways (Souza and Abe 2000; Cadi and Joly 2004; Plummer *et al.* 2008; Ferronato *et al.* 2009; Rees et al 2009; Fagundes *et al.* 2010). As cities continue to grow and urban areas continue to expand, urbanization will come to impact a higher number of turtle populations and more species. Understanding of turtle ecology in these new environments is needed to protect, mitigate and assist the future survival of turtles within urbanized landscapes (Eskew *et al.* 2010a; Roe *et al.* 2011; Stokeld *et al.* 2014).

The main challenges faced by turtles living within urban areas are no different from other vertebrates in similar situations, as turtles are mainly threatened by road mortality, chemical pollution and invasive predators (Gibbs and Shriver 2002; Marchand and Litvaits 2004; Mitchell and Klemens 2000; Marchand *et al.* 2002; Spinks *et al.* 2003; Piña *et al.* 2009; Malik *et al.* 2013). Besides these negative effects of urbanization on some turtle species, there are reports of species taking advantage of increased human-augmented productivity in urban wetlands and end up growing faster, with higher fecundity and abundance than populations from natural settings (Gibbons 1967; Brown *et al.* 1994; Lindeman 1996; Souza and Abe 2000; Roe *et al.* 2011).

Maintenance of functional connectivity is also a key factor influencing persistence of freshwater turtles in urbanized landscapes (Rees *et al.* 2009; Roe *et al.* 2011). The level of connectivity of green spaces in suburbs can predict species richness and occupancy for many species of turtles (Guzy *et al.* 2013). Owing to specific turtle life history traits such as longevity, delayed sexual maturity and low nest survival, any persistent cause of adult mortality, even if small, can have profound consequences for the population (Congdon *et al.* 1993, 1994). Consequently, identification of times and locations of adult turtle mortality within urbanized landscapes are essential for conservation (Cureton and Deaton 2012; Crawford *et al.* 2014). Another essential component in understanding the persistence of turtles in urban areas is the establishment of long-term monitoring programs, as it allows the detection of trends in population dynamics and vital rates over lengths of time consistent with turtle life spans (Plummer and Mills 2008; Plummer *et al.* 2008; Eskew *et al.* 2010b).

Study species

Chelodina longicollis Shaw 1794 (Chelidae) is a common and generalist turtle with a broad geographic distribution in south-eastern Australia, inhabiting a wide variety of habitats throughout its range, including permanent waterholes, lakes, farm dams, shallow temporary ponds, and suburban ponds (reviewed by Kennett *et al.* 2009). One of the distinctive features of this species is its marked propensity for overland movements, which enables it to travel terrestrially and take advantage of a variety of bodies of water, moving between permanent and ephemeral ponds in the wet-dry cycles of south-eastern Australia (Kennett and Georges 1990; Roe and Georges 2008a,b). Such behavior can expose the species to the risk of vehicle mortality while inhabiting suburban areas (Rees *et al.* 2009; Roe *et al.* 2011). *C. longicollis* is not an endangered species and it tends to be abundant within urban-natural gradients (Kennett *et al.* 2009; Roe *et al.* 2011) which make a good model species for the evaluation of anthropogenic impacts on freshwater turtles.

Study system and knowledge gaps

A previous study in Gungahlin region, Australian Capital Territory (ACT), south-eastern Australia, during a drought in 2006-2007, evaluated effects of urbanization in *C. longicollis* in a suburban environment compared to a control group on an adjacent nature reserve (Rees *et al.* 2009; Roe *et al.* 2011). The main findings were that suburban turtles were more abundant, grew faster and had populations comprised of more adults in the larger size classes, than nature reserve populations. This work suggested that suburban ponds were of higher quality than in the surrounding less impacted areas, and that turtles from the nature reserves were attracted to the suburban regions during drought (Roe *et al.* 2011). In addition, suburban turtles were more vagile, moving longer distances than turtles in the nature reserve, and despite the risks of vehicle mortality in the suburb, showed similar survivorship between populations. This was a surprising result, which was attributed to presence of culverts and under-passages where suburban turtles avoided roads and travelled safely using these structures (Rees *et al.* 2009). The authors urged future studies to evaluate long-term responses of *C. longicollis* to urbanization in this system and how the population dynamics and behavior could change during more favourable times, such as wet periods (Rees *et al.* 2009; Roe *et al.* 2011), providing a basis for undertaking the present study.

Our study system has greatly changed since 2006-2007 period (Rees *et al.* 2009; Roe *et al.* 2011), with a sharp increase in urbanization, reflected in a rise in human population and vehicle traffic volume in the suburbs surrounding our study sites (Australian Bureau of Statistics 2013, Territory and Municipal Services) (Fig. 1.1, 1.2, 1.3). Also, climatic conditions have changed: following the long period of drought in south-eastern Australia (Millennium Drought, 2001-2009; van Dijk *et al.* 2013), there was an increase in rainfall influenced by La Niña events from 2010-2012 (Beard *et al.* 2011; BOM 2012). In addition, a predator proof-fence was erected in the nature reserve in 2009 to protect it from encroaching suburban hazards, such as roads, and feral predators (Shorthouse *et al.* 2012), isolating the reserve from the wider landscape (Fig. 1.1, 1.3). Such changes created a unique situation to evaluate the long-term responses of *C. longicollis* to these anthropogenic disturbances and the possible interaction with climate.

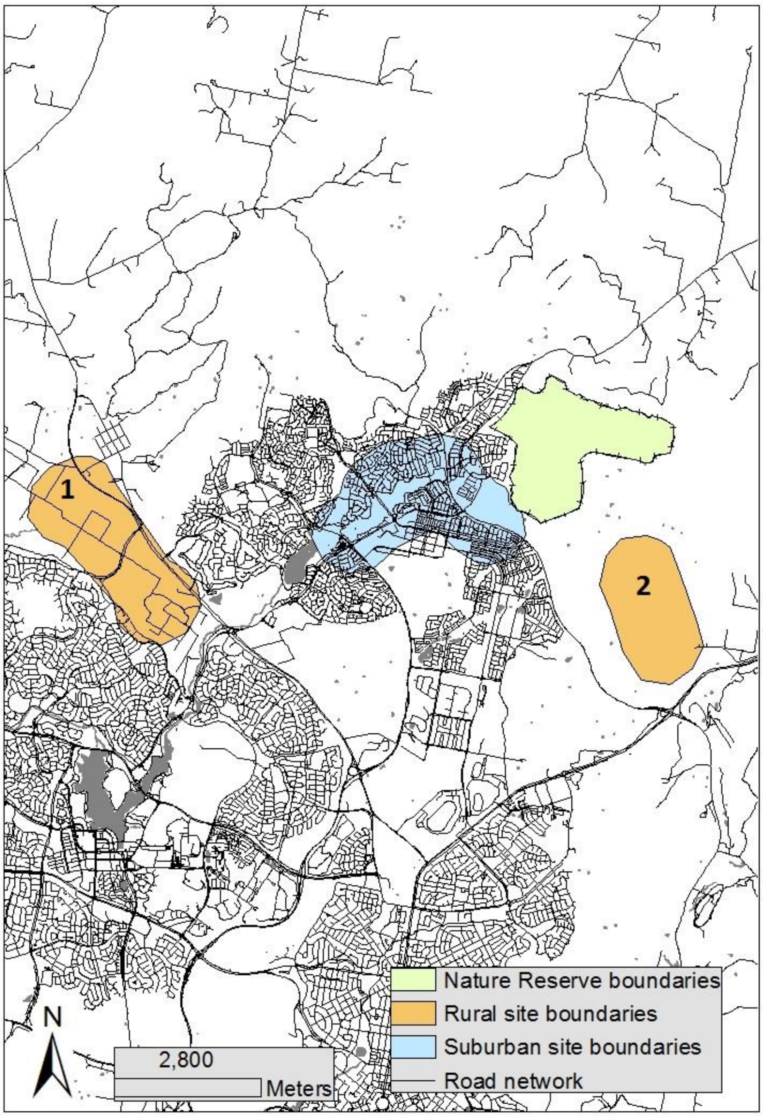

Figure 1.1. Study sites along a natural-urban gradient in Gungahlin region, Australian Capital Territory, southeastern Australia. Mulligans Flat Nature Reserve which is enclosed by pest-fencing is depicted in light green. Number 1 denotes the Ginnindera Experimental Station. Number 2 denotes the Goorooyaroo Nature Park, both part of the rural sites. In light blue is depicted the suburban site in Gungahlin suburbs. Study sites were defined by drawing 700 m polygons around the ponds turtles were trapped and then joining the polygons to delimit each site. The polygons in the nature reserve were expanded to delimit the area protected by pest-fencing.

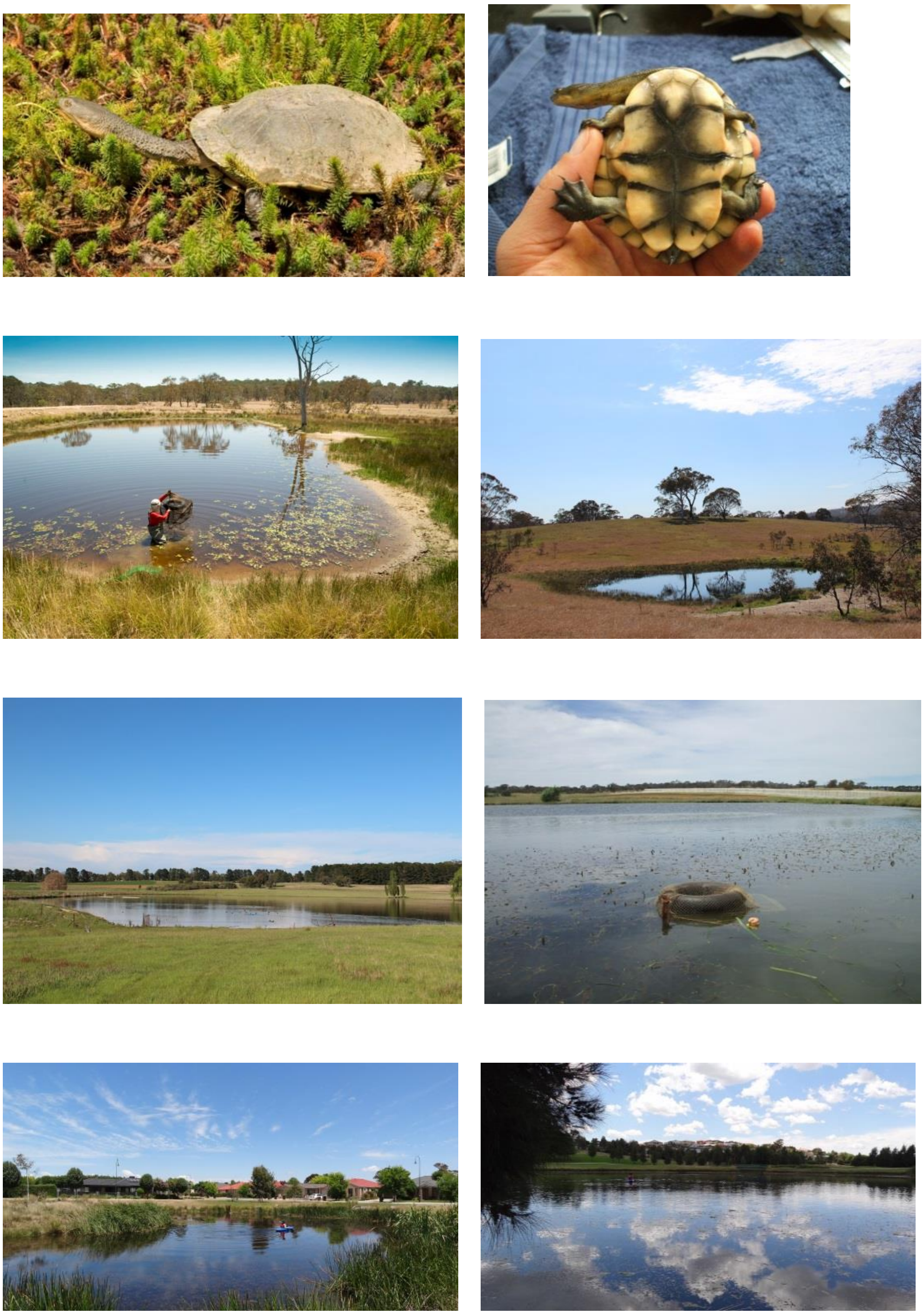

Figure 1.2. Adult and juvenile *Chelodina longicollis* (first row), and the habitats they were studied in Mulligans Flat Nature Reserve (second row) and a rural site (third row), both consisting of ephemeral ponds, and a suburban site (fourth row), consisting of permanent ponds, in Gungahlin region, Australian Capital Territory, Australia. (Photo Credit: Sam Brown, Larissa Schneider, and Bruno Ferronato).

Figure 1.3. Fence monitoring in the nature reserve (top left), and some reptiles found along the fence (*Chelodina longicollis*, top right; *Tiliqua rugosa*, middle left; *Pseudonaja textilis*, middle right) (chapter two). *Chelodina longicollis* nest with an i-button inserted to record nest temperatures (bottom left) and the same nest covered with a metal mesh to avoid predation and monitor the incubation period (bottom right) (chapter five). (Photo Credit: Larissa Schneider and Bruno Ferronato).

Thesis aims and structure

This study aims to evaluate behavioral and population responses in a turtle following changes in the system brought about by increasing urbanization and rainfall relative to earlier studies. Given the benefits of having a marked population in a previous investigation (Rees *et al.* 2009; Roe *et al.* 2011), I could re-evaluate some ecological parameters following such changes, in addition to exploring several new aspects of turtle ecology and behavior. Specifically, my objectives were to 1) understand the effects of a predator-proof fence on a reptile community, with the aim of identify impacts and proposing management actions, 2) to evaluate the spatial ecology and survivorship of adult female *C. longicollis* using radio-telemetry following increased urban development, 3) to investigative demographic responses, vital rates, such as survivorship and fecundity of *C. longicollis* along a natural-urban gradient using capture-mark-recapture, and 4) to investigate the nesting ecology of *C. longicollis* in order to confirm the suspected ability of hatchlings to overwinter in the nest. In the following paragraphs I expand into more details for each of these specific objectives.

In chapter two, I examine the impacts of a predator-proof fence in a non-target reptile community, including not only turtles but also lizards and snakes, as the fence isolated a nature reserve from the wider landscape. The objective is to determine if there is a species-specific impact, the magnitude of the impact at the population level, and identify hotspots and times of major concern, e.g. hot moments of mortality, which could be used by managers for mitigation purposes. This study is essential to put into context how a structure that may block migratory routes and movements could interfere with aspects of population regulation considering the wider landscape in our site.

In chapter three, I use radio-telemetry to evaluate how spatial ecology, movements and survivorship of female turtles within the suburban area compared to females inside of the fence enclosure in the nature reserve. The goal is to evaluate if they differ in spatial ecology, vital rates and behavior, and I also aim to identify hotspots of mortality on city roads.

In chapter four, I use capture-mark-recapture and x-ray analysis to investigate demography, growth rates, fecundity and survivorship of turtles considering populations under different levels of anthropogenic impact. The objective is to re-evaluate vital rates, behavior and population responses to suburban stressors compared to a previous assessment prior to the many changes in the system. This longitudinal study would permit a closer look into the mechanisms involved in persistence of turtles in suburban landscapes, in addition to giving a broader perspective on population vital rates compared to the radio-telemetry study of chapter three.

In chapter five, I examine a more basic aspect of nesting biology of *C. longicollis*, with the aim of documenting incubation period and nesting success in natural nests, and investigate the possibility of overwintering in the nest by hatchlings, owing to anecdotal accounts of such possible behavior in *C. longicollis* in the wild.

Chapter six is a synthesis of the findings in each of the data chapters (chapter two to five), and recommendations of future studies to broaden the insights on the ecology and persistence of freshwater turtles in suburban landscapes.

This thesis is written as a series of papers for publication in scientific journals, except for chapter one and six which serve as introduction and synopsis. Each data chapter is thus formatted following journal-specific guidelines. I have written these chapters with the support and input of my supervisors and co-authors, John Roe and Arthur Georges. As my supervisors, they were fundamental in the planning, guidance, analysis and interpretation of the results in each chapter. Other colleagues that provided advice during the preparation and analysis of these chapters are mentioned in the Acknowledgments.

Chapter 2

Reptile bycatch in a pest-exclusion fence established for wildlife reintroductions

Published as: Ferronato, B.O., Roe, J.H., Georges, A. 2014. Reptile bycatch in a pest-exclusion fence established for wildlife reintroductions. Journal for Nature Conservation 22: 577-585. Presented as published, with minor formatting change.

Abstract

Conservation fences have been used as a tool to stop threatening processes from acting against endangered wildlife, yet little is known of the impacts of fences on non-target native species. In this study, we intensively monitored a pest-exclusion fence for 16 months to assess impacts on a reptile community in south-eastern Australia. We registered 1052 reptile records of six species along the fence. Encounters and mortality were greatest for eastern long-necked turtles (*Chelodina longicollis*), whereas impacts on lizards (*Tiliqua rugosa*, *T. scincoides*, *Pogona barbata*, *Egernia cunninghami*) and snakes (*Pseudonaja textilis*) were more moderate. We recorded several *C. longicollis* recaptures at the fence and many of these were later found dead at the fence, indicating persistent attempts to navigate past the fence. We conservatively estimate that the fence resulted in the death of 3.3% and disrupted movements of 20.9% of the turtle population within the enclosure. Movement disruption and high mortality were also observed for turtles attempting to enter the nature reserve, effectively isolating the reserve population from others in the wider landscape. Of 98 turtle mortalities, the most common cause of death was overheating, followed by predation, vehicular collision, and entanglement. Turtle interactions were clustered in areas with more wetlands and less urban development, and temporally correlated with high rainfall and solar radiation, and low temperature. Thus, managers

could focus at times and locations to mitigate impacts on turtles. We believe the impact of fences on non-target species is a widespread and unrecognized threat, and suggest that future and on-going conservation fencing projects consider risks to non-target native species, and where possible, apply mitigation strategies that maintain natural movement corridors and minimize mortality risk.

Introduction

Conservation fences have been used worldwide as a tool to stop or ameliorate processes that threaten biodiversity (Dickman, 2012; Hayward & Kerley, 2009). Such fences are used to alleviate human-animal conflict, to reduce human persecution on threatened species, and to minimize the impact of introduced species (Hayward & Kerley, 2009). Fences can provide *in situ* protection of threatened species, facilitate the reintroduction of threatened species, and provide opportunity for education, ecotourism and research (Dickman, 2012). Despite their worldwide use, there is a geographic bias in the use of fences for conservation, with many examples in Australia, New Zealand and southern Africa. The threats in Australasia are largely introduced predators, whereas in Africa they arise largely from human-animal conflict (Hayward & Kerley, 2009). Conservation fences can be very effective in protecting and conserving endangered wildlife, with many cases of native species recovery (Dickman, 2012; Hayward & Kerley, 2009).

The use of fences for pest management in Australia has a long history, initially consisting of fences to protect croplands against the European rabbit (*Oryctolagus cuniculus*) and livestock from dingos (*Canis lupus dingo*) (Pickard 2007a; Saunders *et al.*, 2010). More recently, there has been an increase in the use of pest-exclusion fences for conservation purposes in Australia (Bode & Wintle, 2009; Long & Robley, 2004) to protect vulnerable native fauna from invasive predators such as the European fox (*Vulpes*

vulpes), domestic and feral cats (*Felis catus*), and feral pigs (Doupé *et al.*, 2009; Hayward & Kerley, 2009; Long & Robley, 2004; Moseby & Read, 2006).

Pest-exclusion fences have clear conservation benefits for populations of endangered animals by controlling the spread of diseases from domestic to wild populations, excluding exotic predators or competitors, and reducing human-animal conflicts (Hayward & Kerley, 2009). However, the fences themselves can negatively impact non-target native wildlife by disrupting natural movement and dispersal processes, increasing mortality via entanglement and exposure, and enforcing inbreeding and isolation (Bode & Wintle, 2009; Flesch *et al.*, 2010; Hayward & Kerley, 2009; Long & Robley, 2004). Fences are also costly to build and maintain, with an opportunity cost for other conservation and management priorities (Scofield *et al.*, 2011).

While there are some reports of impact of fence design and alignment on select native mammal and bird populations (Hayward & Kerley, 2009; van der Ree, 1999), information on the impact of fences on reptiles is limited. Reptile mortality has been observed in feral animal-exclusion fences in Australia (Kuchling, 2000; Long & Robley, 2004) and South Africa (Burger and Branch, 1994), particularly turtles, but the magnitude of the impact of such fences and the circumstances that trigger encounters and mortalities remain unclear. The impact of such fences could be highest for vagile animals, as species requiring frequent movements are more likely to encounter fencing and become isolated from critical resources or exposed to mortality risk. One such species that is common in our study system is the eastern long-necked turtle (*Chelodina longicollis*), which travels overland to nest, estivate, and move between wetlands in response to wet-dry cycles – behaviors that are essential for survival of individuals and the elements of population dynamics that support their persistence (Rees *et al.*, 2009; Roe *et al.*, 2009). Other mobile terrestrial species, such as large lizards and snakes, may also be disturbed by a fence and suffer high mortality, as they also move extensively through the landscape (Cogger, 2000; Fergusson & Algar, 1986; Price-Rees *et al.*, 2012; Whitaker & Shine, 2003).

Here, we evaluate how a pest-exclusion fence affects non-target wildlife at a site in south-eastern Australia. We assess the effect of fences on movements and mortality in a reptile community, and environmental factors that explain these parameters that may be used to predict times and locations of highest concern. Such information can guide land managers in mitigating the impact of fences on non-target native wildlife, and in better assessing the trade-off between costs and benefits of fence projects.

Method

Study area

Our study site was in Mulligans Flat Nature Reserve, located in the Australian Capital Territory (ACT) of Australia. The 791 ha reserve is part of a large-scale woodland restoration project (Manning *et al.*, 2011), around which an 11.5 km-long pest-exclusion fence was constructed in 2009. The fence design was based on similar fences in Australia (Moseby & Read, 2006). The fence is electrified and stands 1.8 m high with seven plain wires supporting rabbit mesh (30 mm), with a 60 cm “floppy overhang” and netting buried to a width of 45 cm on either side (Fig. 2.1). Several self-closing gates are placed in the fence perimeter which allows visitors and park maintenance staff to pass (Shorthouse *et al.*, 2012). The goal of the pest-exclusion fence is to protect native fauna and flora within the fenced boundaries, to facilitate re-introduction of locally extirpated species, including the Eastern Bettong (*Bettongia gaimardi*) and the Southern Brown Bandicoot (*Isoodon obesulus*), and to exclude the introduced fox, domestic cats and dogs,

Figure 2.1. Pest-exclusion fence at Mulligans Flat Nature Reserve, Australian Capital Territory, Australia (Photo Credit: Larissa Schneider).

as well as hares and rabbits from the sanctuary (Manning *et al.*, 2011; Shorthouse *et al.*, 2012).

Fence monitoring

We monitored the fence by slowly driving (15 km/hr) along an adjacent service road, which is located 2 m away from the fence. Information on turtle encounters was collected from January 2012 to April 2013 and expanded to include lizards and snakes from March 2012 to April 2013. We monitored the fence twice per week during the season when reptiles are typical active (Sep – Apr), and once per month during the overwintering period (May – Aug).

Whenever a reptile was sighted by the fence, we identified the species and registered its location using a hand-held GPS unit (Garmin 43434) and recorded its position along the fence (inside / outside) and its status (dead, injured, alive). We recorded encounters up to 10 m away from each side of the fence. If the animal was dead, we recorded the likely cause from external evidence observed on the animal (damage, lesions) or on the basis of context (entrapped, overheated, crushed). All dead reptiles were removed from the fence.

We marked turtles with unique codes by notching the shell (Kennett & Georges, 1990), and measured maximum carapace length (CL) and midline plastron length (PL) with callipers (± 0.1mm) and body mass with a scale (± 5 g). Turtles with a CL < 145 mm were considered juveniles; those for which CL > 145 mm were classified as males or females on the basis of external morphological features (see Kennett & Georges, 1990). We did not mark or measure lizard and snakes, as our intention for these groups was not to estimate the number of animals affected by the fence, but instead to record frequency of encounters to determine location and time-specific hotspots and hot moments. All live animals were released at their point of capture on the same side of the fence.

Pond sampling

To assess the magnitude of impact for the fence on the wider population, we surveyed turtles from a subset of ponds in the fence vicinity. We trapped turtles in five nature reserve ponds inside the fence and three ponds outside of the fence. In each pond, we set four traps baited with sardines and liver once per month (5 consecutive days of trapping per month) from January 2012 to March 2013. More details on trapping methods are discussed by Roe *et al.* (2011). Turtles in the ponds were marked and measured in the same way as along the fence.

Data analysis

Statistical analyses were performed with SPSS (Version 21) and SAS Version 9.1 (SAS Institute, 1999). The assumptions of normality and homogeneity of variances were checked by analysis of residuals and when data failed to meet these assumptions, data were transformed to approximate normal distributions and equal variances. Statistical significance was accepted at the $\alpha = 0.05$ level unless specified otherwise.

To assess spatial distributions of encounters, we plotted encounter records on a map of the fence using the ArcGIS (version 9.3.1: ESRI, 2009). We then divided the fence into 500 m sections, resulting in 23 fence segments. Records of wildlife encounters were then summed by species and fence position (inside/outside) within each segment. To examine if reptiles had a random or non-random distribution around the fence, we used chi-square tests with the null-hypotheses that abundance of records within each fence segment would be equal.

To assess spatial correlates of reptile encounters (i.e. hotspots) within each fence segment, we selected the segment midpoint and created a polygon with 700 m radius. This distance was based on typical movement distances of *C. longicollis* determined from previous studies in the region, which would also cover the range of the other reptile species with smaller home ranges (Fergusson & Algar, 1986; Rees *et al.*, 2009; Roe & Georges, 2007; Roe *et al.*, 2009). We used a vegetation map developed by Rees *et al.* (2009), with corrections using a 2012 aerial photograph. We then measured the area coverage of five land cover types (farmland, grassland, woodland, wetland, and urban development) and calculated correlations with number of animals encountered inside plus outside within each polygon. We performed multiple stepwise linear regressions to asses if the land cover variables (predictor variables) were associated with number encountered (response variable). In the above analysis, we log (ln) transformed all abundance estimates.

To assess temporal distributions of encounters, we summed the species records monthly. To determine if temporal distribution of records were random or non-random, we used chi-square tests with the null-hypotheses that abundance of records within each month would be equal. To examine correlates of temporal distributions of encounters with environmental variables (i.e. hot moments), we considered reptile encounters (alive and dead) in relation to daily maximum temperature (°C), rainfall (mm) and daily solar exposure (MJ/m^{-2}). We considered the number of reptile records in the fence within an interval of 15 days. We used the mean value for the 15-day period for daily maximum temperature and daily solar exposure, and for rainfall we used the amount accumulated over the period. We then performed multiple stepwise linear regressions to determine the best supported model of association between the environmental variables and the number of individuals encountered for each species. We log (ln) transformed turtle records and square root (sqrt) transformed lizard to better meet assumptions.

To assess if variables would influence mortality, we performed a logistic regression using dead turtle encounters as the response variable. As explanatory variables we considered location (inside or outside of the fence), season (summer 2012, autumn 2012, winter 2012, spring 2012, summer 2013, and autumn 2013), sex (male, female, juvenile), carapace length (cm), daily maximum temperature (°C), rainfall (mm), and daily solar exposure (MJ/m^{-2}). We considered an interval of 15 days for each of these environmental variables as described above.

To examine whether fence bycatch risk depended upon demographic group, we compared size-frequency distributions and sex ratios of turtles encountered inside *versus* outside the fence, in addition to all turtles from the fence (inside plus outside) *versus* those trapped in ponds in the vicinity of the fence. Size-frequency distributions were compared with a chi-square test with the null hypothesis of equal frequency between samples for all size class groups. We followed the overall test with a series of chi-square tests to determine where specific differences existed. We lowered significance values for this series of comparisons to $\alpha < 0.005$ using the Dunn-Sidak correction for avoiding false positives arising from compounding error. We performed chi-square tests to examine differences in sex ratios between turtles encountered at the fence *versus* ponds, and the inside *versus* outside of the fence.

To estimate the magnitude of fence bycatch on turtles at the population level, we estimated population size (mean ± SE) within the five sampled nature reserve ponds using the Horvitz-Thompson type estimator $N = (n/p)$, where N is the estimated population abundance, n is the number of turtles captured and p is the estimated recapture probability (Seber, 1982). We used recapture probabilities derived from previous studies using similar trapping protocols in the same study system (Roe *et al.*, 2011).We then calculated population density (number/ha) in the five surveyed ponds and extrapolated density estimates to all ponds within the fenced area to obtain a within-reserve population size estimate.

Results

Encounters and mortalities

We encountered six species during fence surveys, totalling 1052 reptile encounters, with *C. longicollis* the most common species followed by shingleback lizards (*Tiliqua rugosa*), eastern bearded dragon lizards (*Pogona barbata*), blue tongue skinks (*Tiliqua scincoides*), eastern brown snakes (*Pseudonaja textilis*), and Cunningham's skinks (*Egernia cunninghami*) (Table 2.1).

Of 108 dead animals encountered, the majority were *C. longicollis* (90.7%), followed by *T. rugosa* (4.6%), *P. barbata* (2.8%), *T. scincoides* (0.9%) and *P. textilis* (0.9%). The most common cause of death in *C. longicollis* was overheating (n = 68; inside = 10, outside = 58), followed by fox depredation (n = 18; inside = 0, outside = 18), vehicular collision (n = 10; inside = 10, outside = 0), and entanglement (n = 2; inside = 1, outside = 1). Overheated turtles had signs of skin sunburn, mouth opened and neck and hyoid extended. Turtles depredated by foxes had the limbs and/or head eaten, though these signs may also suggest scavenging by foxes. Five *T. rugosa*, one *P. barbata* and one *T. scincoides*, all adult individuals, died from overheating; one *P. textilis* died from entanglement; and two *P. barbata* died from electrocution. We recaptured several *C. longicollis* along the fence. Of the 71 *C. longicollis* recaptured alive, 68% were captured twice, 27% three times, 4% four times, and 1% five times. Fifty *C. longicollis* were recaptured and eventually found dead (70% on the second recapture, 16% on the third

Table 2.1. Live and dead reptile encounters in the pest-exclusion fence at Mulligans Flat Nature Reserve, Australian Capital Territory, Australia.

	Records along the fence			Deaths along the fence		
	Inside	Outside	Total	Inside	Outside	Total
Chelodina longicollis	211	361	572	21	77	98
Tiliqua rugosa	251	106	357	5	0	5
Pogona barbata	81	22	103	1	2	3
Tiliqua scincoides	10	6	16	1	0	1
Pseudonaja textilis	3	0	3	1	0	1
Egernia cunninghami	1	0	1	0	0	0

recapture, 12% on the fourth recapture, and 2% on the sixth recapture), indicating persistent attempts to navigate past the fence.

Spatial correlates of encounters

Encounters were not equally distributed among the fence segments for any species (*C. longicollis*: $X^2 = 1158.6$, df = 22, $p < 0.001$; *T. rugosa*: $X^2 = 75.1$, df = 22, $p < 0.001$; *P. barbata*: $X^2 = 89.7$, df = 22, $p < 0.001$) (Fig. 2.2). *Chelodina longicollis* encounters were positively correlated with total wetland area and negatively correlated with urban development area, explaining 51% of the variation ($F_{2, 19} = 9.90$, $r^2 = 0.51$, $p < 0.001$) (Predictor variables: Wetland area: Beta = 0.55, $p = 0.003$; Urban development area: Beta = -0.37, $p = 0.035$). However, *T. rugosa* ($F_{4, 18} = 2.34$, $r^2 = 0.34$, $p = 0.09$) and *P. barbata* ($F_{4, 17} = 2.77$, $r^2 = 0.39$, $p = 0.06$) encounters were not correlated with any of the measured land cover variables.

Temporal correlates of encounters

Encounters were not equally distributed among months (*C. longicollis*: $X^2 = 677.2$, df= 15, $p < 0.001$; *T. rugosa*: $X^2 = 1193.2$, df = 13, $p < 0.001$; *P. barbata*: $X^2 = 158.9$, df = 13, $p < 0.001$) (Fig. 2.3). *Chelodina longicollis* encounters were positively correlated with daily solar exposure and rainfall, and negatively correlated with daily maximum temperature, explaining 70% of the variation ($F_{3, 20} = 15.72$, $r^2 = 0.70$, $p < 0.001$) (Predictor variables: daily solar exposure: Beta = 1.63, $p < 0.001$; daily maximum temperature: Beta = -1.32, $p < 0.001$; rainfall: Beta = 0.32, $p = 0.020$). *Tiliqua rugosa* encounters were positively correlated with daily solar exposure, and negatively correlated with daily maximum temperature, explaining 48% of the variation ($F_{2, 26} = 11.80$, $r^2 = 0.48$, $p < 0.001$) (Predictor variables: daily solar exposure: Beta = 1.21, $p < 0.001$; daily maximum temperature: Beta = -0.73, $p = 0.014$). *Pogona barbata* encounters were

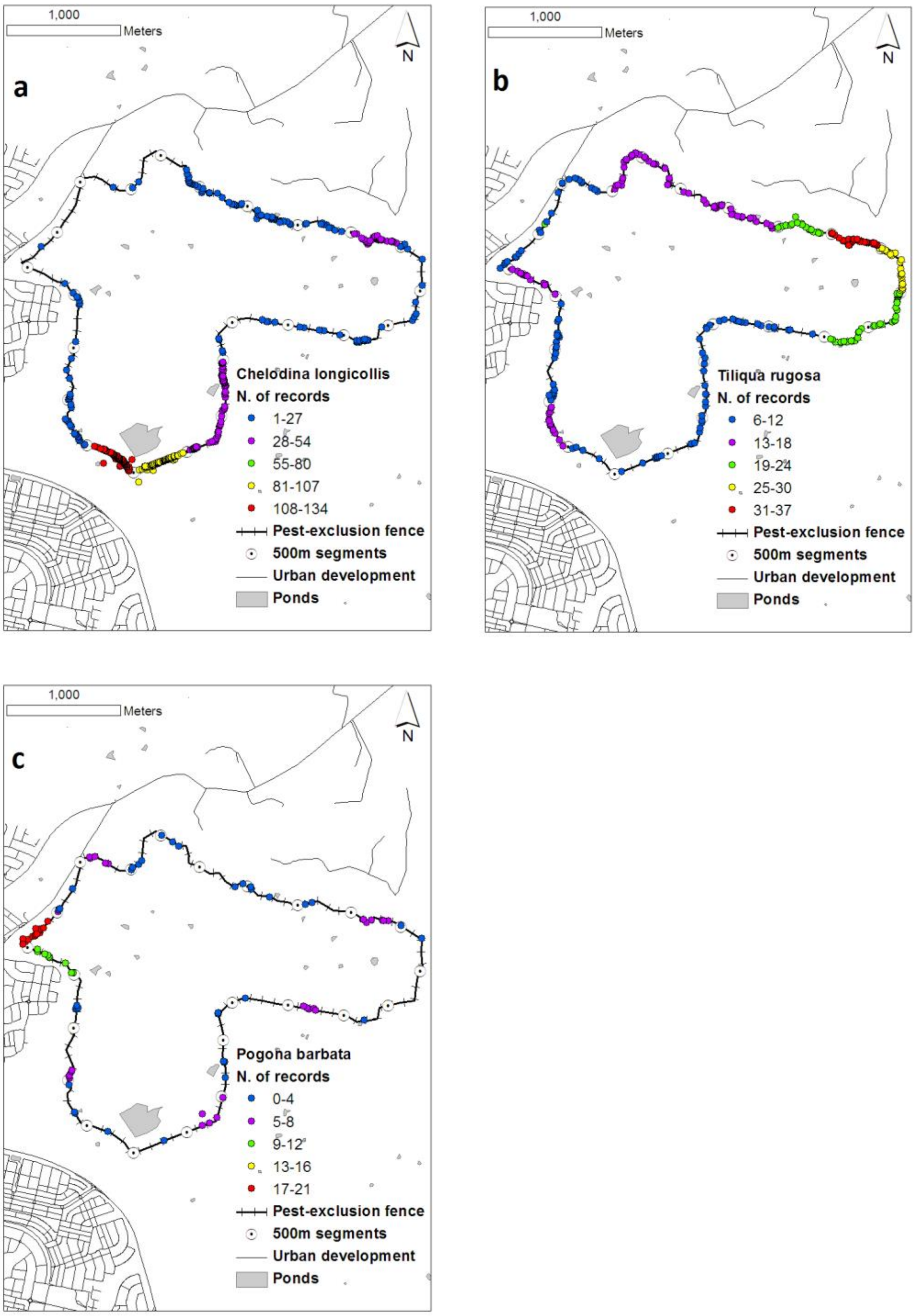

Figure 2.2. Spatial distribution of encounters for **a** *Chelodina longicollis*, **b** *Tiliqua rugosa*, and **c** *Pogona barbata* along the pest-exclusion fence at Mulligans Flat Nature Reserve, Australian Capital Territory, Australia. Each point represents a unique animal encounter, color-coded to reflect the number of encounters occurring within the 23 fence segments.

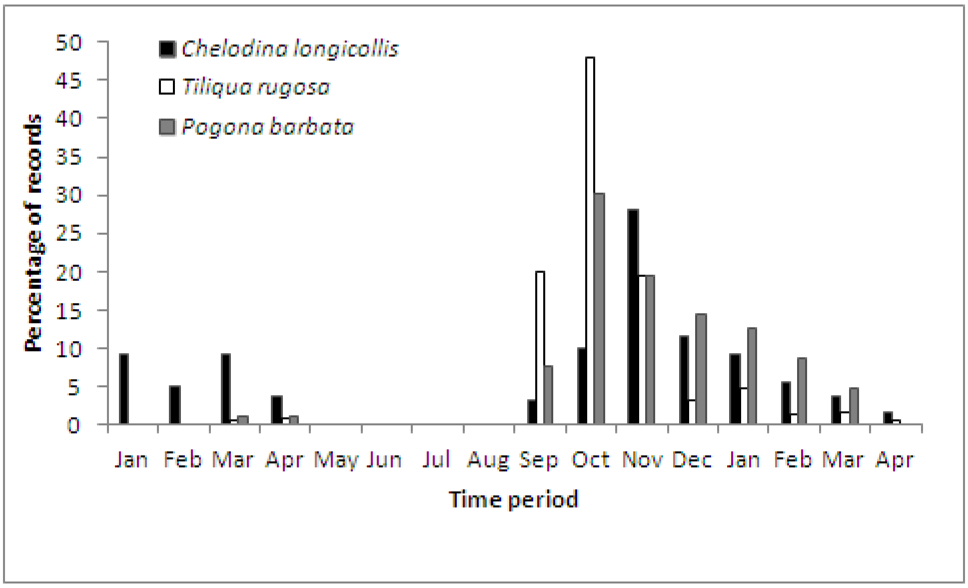

Figure 2.3. Temporal patterns of reptiles records from Jan 2012 to Apr 2013 in the pest-exclusion fence at Mulligans Flat Nature Reserve, Australian Capital Territory, Australia.

positively correlated with daily solar exposure and rainfall, explaining 70% of the variation ($F_{2, 26} = 31.10$, $r^2 = 0.70$, $p < 0.001$) (Predictor variables: daily solar exposure: Beta = 0.79, $p < 0.001$; rainfall: Beta = 0.29, $p = 0.012$).

Our logistic regression model identified location ($p = 0.002$), season ($p = 0.004$), daily maximum temperature ($p < 0.001$), rainfall ($p = 0.001$), and daily solar exposure ($p < 0.001$) as predictors of *C. longicollis* mortality along the fence (Table 2.2). Turtles had a higher chance of dying on the outside of the fence, and a lower probability of dying during Autumn and Spring. Mortalities were positively correlated with daily maximum temperature and daily solar exposure, but negatively correlated with rainfall (Table 2.2).

Size-frequency distributions

Size-frequency distributions differed between turtles encountered at the fence and pond captures (overall $X^2 = 27.68$, df = 10, $p = 0.002$), but the only significant disparity occurred within the 60.1 – 75mm PL size class ($X^2 = 11.5$, df = 1, $p < 0.005$) (Fig. 2.4). Female encounters at the fence were similar to ponds, while males were 1.6 times more commonly found at the fence compared to pond captures ($X^2 = 13.54$, df = 2, $p = 0.001$). Frequency of encounters for turtles on the inside and outside of the fence did not differ for any demographic group (size-frequency distributions: $X^2 = 7.81$, df = 8, $p = 0.45$), or sex and age class ($X^2 = 0.56$, df = 2, $p = 0.75$) (Fig. 2.4).

Magnitude of disruption

Turtle population density within the five sampled ponds was 77 individuals/ha (range: 56 - 125), which extrapolates to an estimated population size of 641 (range: 466 – 1041) within the fenced reserve. Movements were disrupted for 20.9% (range: 12.9 – 28.8%) of the reserve population, with 3.3% (range: 2.0 – 4.5%) of the population killed along the fence.

Table 2.2. Logistic regression model base for timing of *Chelodina longicollis* deaths along the pest-exclusion fence at Mulligans Flat Nature Reserve, Australian Capital Territory, Australia.

	B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I.for EXP(B)	
							Lower	Upper
Location(1)	1.650	0.536	9.483	1	0.002	5.209	1.822	14.894
Season			15.442	4	0.004			
Season(1)	-13.236	4164.478	0.000	1	0.997	0.000	0.000	.
Season(2)	-5.543	1.411	15.435	1	0.000	0.004	0.000	0.062
Season(3)	-5.482	1.483	13.654	1	0.000	0.004	0.000	0.076
Season(4)	-19.612	6001.747	0.000	1	0.997	0.000	0.000	
SEX			2.627	2	0.269			
SEX(1)	-0.080	0.537	0.022	1	0.881	0.923	0.322	2.644
SEX(2)	0.520	0.545	0.909	1	0.340	1.682	0.578	4.897
CL[a]	-0.027	0.082	0.107	1	0.744	0.974	0.829	1.143
DMT[b]	0.421	0.117	12.949	1	0.000	1.523	1.211	1.915
Rain[c]	-0.088	0.026	11.329	1	0.001	0.916	0.871	0.964
DSE[d]	0.665	0.156	18.122	1	0.000	1.944	1.432	2.641
Constant	-25.880	5.519	21.988	1	0.000	0.000		

[a] CL= carapace length; [b] DMT= daily maximum temperature; [c] Rain= rainfall accumulated; [d] DSE= daily solar exposure

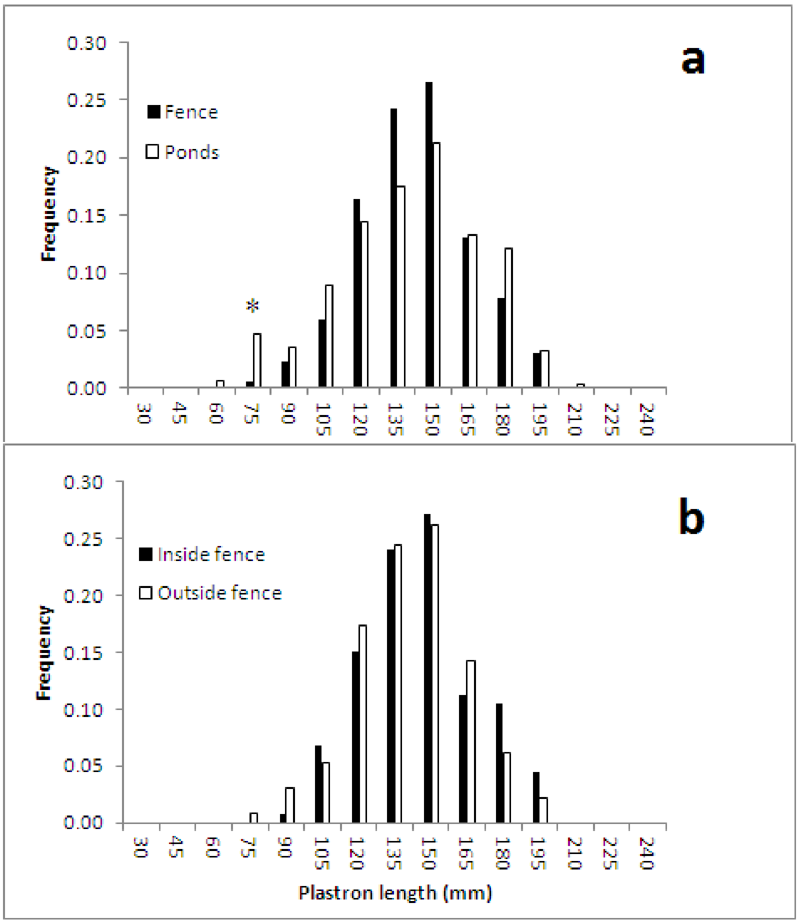

Figure 2.4. Size-frequency distributions of *Chelodina longicollis* **a** captured in ponds compared to those moving along a pest-exclusion fence, and **b** those that were found inside of the pest-exclusion fence compared to those outside at Mulligans Flat Nature Reserve, Australian Capital Territory, Australia. Asterisk indicates size class that differed in frequency of occurrence between sites, adjusted to $\alpha < 0.005$.

Discussion

To our knowledge, this is the first quantification of the impact of a pest-exclusion fence on a reptile community, and one of the most detailed studies on the impact of fences in non-target species. Our main findings relative to feral pest management were that (1) several non-target native wildlife species had their movements restricted by the fence; (2) impacts were most severe for turtles, both in fragmenting local populations by disrupting movements and causing mortality at levels likely to threaten long-term population viability; and (3) encounters and mortalities were predictable in space and time, which would allow for species-specific management of fence bycatch. Together, these findings suggest that current and future fence designs that do not consider the ecology of non-target species can lead to negative consequences for populations of native wildlife.

General impacts on reptiles

The current design of the pest-exclusion fence precluded movements of native wildlife of several species of large lizards and snakes, but impacts were most severe for turtles. While it is possible that such variation reflects relative population sizes of species in the area, it is more likely that the placement of the fence interferes with differences in important species-specific movement routes. One might expect that a terrestrial fence would have little impact on a nominally aquatic species of turtle. However, *C. longicollis* moves overland for nesting, to locate terrestrial refugia for estivation, and during movements among wetlands (Kennett *et al.*, 2009; Roe & Georges, 2007; Roe *et al.*, 2009). The large proportion of the population encountered at the fence representing all demographic groups from regional wetlands underscores the importance of such movements for *C. longicollis* population. A structure blocking their path would thus disrupt natural behaviors, potentially reducing survival directly or restricting access to critical resources. The lizards and snake species found by the fence occasionally move large distances, but in general they exhibit small home ranges (Fergusson & Algar, 1986; Price-Rees *et al.*, 2012; Whitaker & Shine, 2003). Considering the relatively low number of lizard and snake encounters and mortalities, it is likely that the fence is less restrictive of their movements compared to turtles.

Most of the turtle records were on the outside of the fence clustered in a few regions along the fence perimeter (Fig. 2.2), suggesting turtles were attempting to access habitats and resources within the reserve. Previous research in this system revealed that, before the fence was built, drought conditions forced many turtles to move from the nature reserve into the larger suburban ponds for refuge (Rees *et al.*, 2009; Roe *et al.*, 2011), opposite the predominant direction we observed in our study. During drought, water levels in the nature reserve ponds tend to fluctuate more and experienced greater drying than the suburban ponds (Rees *et al.*, 2009). The attempted movements back into the reserve are likely in response to the reflooding of wetlands following considerably more rainfall during and just prior to the current study (study period rainfall: 965 mm, Australian Bureau of Meteorology) compared to previous years (649 mm, Australian Bureau of Meteorology) (Rees *et al.*, 2009; Roe *et al.*, 2011). Such two-way movements between permanent and ephemeral water bodies are key elements affecting survival and regional carrying capacity of *C. longicollis* in response to wet-dry cycles (Kennett *et al.*, 2009; Rees *et al.*, 2009; Roe & Georges, 2007; Roe *et al.*, 2009, 2011), and the fence is completely disrupting this dynamic. Any animals that require extensive movement through the landscape would be severely impacted by exclusion fencing, as such barriers can disrupt population and metapopulation dynamics, gene flow, and population rescue from stochastic events (Boonstra & Krebs, 1977; Epps *et al.*, 2005; Flesch *et al.*, 2010; Krebs *et al.*, 1969; Lesica & Allendorf, 1995; Marsh & Trenham, 2001).

In addition to being an impenetrable barrier, the fence also caused considerable indirect mortality in *C. longicollis*. Overheating was the presumed primary cause of death, as areas around the fence offered little refuge for turtles, which can result in rapid overheating when exposed to unsuitable conditions. Critical thermal maximum for turtles occurs at around 40°C (Hutchison *et al.*, 1966), and prolonged (> 1 hr) central body temperatures > 38°C can lead to dehydration and eventual death (Lagarde *et al.*, 2012). As would be expected, days with higher temperatures and solar index, and little to no rainfall resulted in the highest probability of turtle mortality. Entanglement was not a major cause of mortality in our study site, being responsible for only two cases in turtles and one in snakes. Mesh sizes in Australia (30 mm hexagonal netting) are mainly framed to protect native species against large predators, such as cats, rabbits and foxes, while mesh sizes in New Zealand are smaller (6 x 50 mm), as small mammals (house mice) are the main threat to native species (Moseby & Read, 2006; Burns *et al.*, 2012). A larger mesh size would probably not be desirable as they would allow juvenile rabbits to pass through (Moseby & Read, 2006). A possible reduction in mesh somewhere between these two measurements above could help to prevent entanglement, though this would need to be experimentally tested.

We observed that many turtles were recaptured at the fence several times, only to be eventually found dead, demonstrating that they repeatedly attempted the movement despite the obstacle. We conservatively estimate that the fence caused mortality in 3.3% (2.0 – 4.5%) of the reserve turtle population during the period of our study. These numbers are likely an underestimate of the actual impact of the fence on turtles at the population-level, considering many dead turtles would have gone undetected by observers due to scavenging and observer bias. Moreover, many turtles found outside the fence were likely part of the reserve population in the process of migrating back to the reserve following the end of drought, as *C. longicollis* populations here and elsewhere move among several water bodies with groups of permanent and temporary wetlands harboring the most relevant population unit (Roe *et al.*, 2009, 2011). Even with the uncertainty of these estimates, such mortality (if chronic) is likely to threaten long-term population viability in turtles (Brooks *et al.*, 1991; Congdon *et al.*, 1993; Heppell, 1998). While there may be some benefits for turtles within the pest-exclusion zone via relief from fox predation on nests (Spencer, 2002; Thompson, 1983), the number of adult deaths observed here would likely still drive population declines (Congdon *et al.*, 1993) and limit recovery following stochastic events such as drought. Ironically, fox depredation on turtles was high along the fence designed to protect wildlife from the foxes.

Management, mitigation and non-target species

Our investigation demonstrates that fences can affect non-target species and management is going to be most effective when the behavior and population dynamics of native species in the system are considered during threat/risk assessments. Establishing pest-proof fences in National Parks (e.g. Booderee NP, see Roe & Georges, 2007) or other protected areas set aside for native species conservation and maintenance of natural system functioning can be questioned in some cases. Perhaps such fences would be best established adjacent to protected areas of high value where they will, through concurrent habitat improvement, raise conservation value more generally and achieve benefits beyond feral predator control. Also, the rationale for the fence establishment should be evaluated in terms of balancing costs and benefits for target and non-target species. We acknowledge that conservation fences can be the only option for the conservation of some native species due to the enormous effect of introduced mammalian predators (Dickman, 2012; Dowding & Murphy, 2001; Hayward & Kerley, 2009). Perhaps in cases where fences are constructed for *in situ* protection of remnant populations of endangered species and time is a limiting factor to halt the threatening processes, one could limit costs to non-target species by fully implementing mitigation strategies to reduce the impact on them. Nonetheless, in the case of reintroduction of locally extinct fauna, managers still have time to consider and balance costs and benefits. In such situations, fences should be erected only in areas where they pose a minimum risk to non-target species.

There is a current debate in New Zealand, a country with tradition in the use of conservation fences, over whether predator-proof fences are the best management option to conserve native species against feral animals, with some suggesting conservation fences are not cost-effective over the long-term, and that the fence projects frequently do not achieve the goals of species conservation and recovery (Scofield *et al.*, 2011). Others proclaim the benefits of predator-proof fences and cite several examples of species recovery and feral pest exclusion, pointing out that fence projects can also provide social and education benefits, an infusion of funding from non-traditional sources, and powerful advocacy on behalf of other conservation initiatives (Innes *et al.*, 2012). Adding to such discussions, Norbury *et al.* (2014) recently evaluated cost-effectiveness of pest fencing *versus* pest trapping in New Zealand, finding that predator proof-fences are most cost-effective for areas below 1 ha, semi-permeable (“leaky”) fences are most cost-effective for 1-219 ha, and trapping is the most cost-effective for areas above 219 ha (Norbury *et al.*, 2014).

Conservation fences are clearly an effective management practice in many circumstances (Dickman, 2012; Hayward & Kerley, 2009), including some cases in which fences were erected specifically to protect turtles and their habitats (Doupé *et al.*, 2009; Kuchling, 2000). For a successful implementation of conservation fences, managers require specific information to guide them in fence construction and maintenance. In addition, managers need to prioritize sites for localized mitigation measures (i.e. hotspots) and periods when threat rates are highest (i.e. hot moments) as such strategies reduce the risk of mortality and are essential to the long-term survival of native species in challenging landscapes (Beaudry *et al.*, 2008, 2010). In our system, the fence layout should avoid bisecting travel routes among wetlands, and based on the movement capacity of *C. longicollis*, this should include distant wetlands up to 1.5 km away (Roe & Georges, 2007; Roe *et al.*, 2009). Where potential disruptions to movements cannot be avoided, mitigation to facilitate movements and avoid mortality could be applied at targeted times and locations, in accordance with our analysis, including: (1) manually assisting animals across the fence at hot moments for mortalities (perhaps using volunteers), (2) conducting a poison bait program for foxes (Long & Robley, 2004) along animal hotspots, (3) regularly mowing the vegetation close to the fence and covering the puddles with gravel to increase driver visibility and reduce the chances of vehicular mortality, and (4) building aquatic under-passages (Long & Robley, 2004) or size-specific mesh (Roe & Georges, 2007) along animal hotspots that facilitate non-target animal movements while excluding pests. However, the purpose of our study was not to test effective solutions. Encouragingly, managers have been presented with other threats to turtles, such as fisheries bycatch and roads (Brewer *et al.*, 2006; Gibbs & Shriver, 2002; Lewison & Crowder 2007) and through careful study, progress has been made towards implementing successful solutions, at least on local scales (Beaudry *et al.*, 2008; Brewer *et al.*, 2006; Dodd *et al.*, 2004; Lewison & Crowder, 2007). We are not suggesting that fencing is a problem of equal magnitude to roads and fisheries bycatch, but it is nonetheless a parallel scenario that warrants action, and it is not an intractable problem. While the decisions of whether or not to build a fence and which mitigation practices to employ are likely to be complex and unique to each fence project, our study nonetheless provides an example of the process to help inform managers of potential conflicts and solutions.

Conclusion

Although we focused on a single conservation fence, we believe that the impact of fences on non-target species is widespread in Australia and elsewhere. In Australia alone, there are at least 37 pest-exclusion fences projects enclosing 136,342 ha (Dickman, 2012; Long & Robley, 2004), and other large fence enterprises include the dingo fence covering 5,631 km (Allen & Sparkes, 2001), the rabbit proof fence extending 3,256 km (Prober & Smith, 2009), and the emu proof State Barrier Fences extending 1,170 km (Pickard, 2007b). Additionally, there are countless other undocumented kilometres of rural fencing to protect agriculture and livestock, but the current length is unknown (Pickard, 2007a). Anecdotal evidence on the mortality of turtles in sheep farms was brought to us by farmers in the region, and we have observed turtle entanglement in such fencing previously (J.H.R. and A.G., personal communication), in addition to reports of turtle death against rabbit fencing in Victoria, Australia (Anon., 1941). Pest-exclusion fencing is common in other countries as well, including at least 31 such fences enclosing 9,160 ha in New Zealand (Burns *et al.*, 2012; Scofield *et al.*, 2011) and Zimbabwe, where veterinary fences extend for 2,250 km (Taylor & Martin, 1987). All of these types of fences have the potential to exclude and kill native vertebrates, and continued implementation of this widespread and popular conservation and management practice should be critically examined to avoid further collateral damage.

Chapter 3

Urban hazards: spatial ecology and survivorship of female turtles in an expanding suburban environment

The manuscript has been submitted for publication in the journal **Urban Ecosystems** as: Ferronato, B.O., Roe, J.H., Georges, A (*in review*). Urban hazards: spatial ecology and survivorship of a turtle in an expanding suburban environment. Presented as submitted, with minor formatting changes.

Abstract

Urbanization is a leading cause of biodiversity loss worldwide. We studied movements, behavior and survivorship of females of a semi-aquatic turtle, *Chelodina longicollis*, in a natural-urban gradient, during a La Niña period of above average rainfall. Our goals were to compare these attributes for turtles in a suburban environment to those in an adjacent nature reserve, and to compare our results to those of a previous study in the same system during an El Niño period of drought. During the period of above average rainfall, female turtles from suburban and nature reserve environments had similar movements and spatial metrics, except for total distances moved. Turtles did not enter terrestrial aestivation in any of the sites during the wet period, unlike prolonged periods of terrestrial aestivation during the previous drought in the nature reserve. Considering size of ponds as a factor, turtles from smaller ponds used more wetlands than turtles from larger ponds, exposing them to increased risks from vehicular mortality during overland movements. Turtles from suburbs had reduced annual survivorship (0.67) compared to turtles in the nature reserve (1.00), which contrasts with previous drought when survivorship did not differ between environments. Such a reduction in survivorship for suburban turtles resulted largely from vehicular collisions and may be ultimately attributed to rapid increases in human population (79.2%) and traffic volume (76%) over the five-year period between studies. Our study demonstrates that turtle behavior and survivorship are variable in space and time, and that both urban development and climatic conditions can interact and change relatively quickly to influence important aspects of turtle behavior and population biology.

Introduction

Urbanization is one of the leading causes of biodiversity loss and local extinction (McKinney 2002, 2006; Shochat *et al.* 2006). Such an aggressive form of habitat alteration and land conversion results from a complete restructuring of landform, vegetation and species composition (McKinney 2002; Miller and Hobbs 2002). Cities are dynamic entities (Button 2002), where human population growth, urban sprawl and increase in road traffic are expected for many cities worldwide, especially in developing countries (World Resources Institute *et al.* 1996; Gakenheimer 1999; Schafer and Victor 2000). Biologically, urban environments typically show a pattern of reduced native species richness and an increase in abundance for urban-tolerant species (Shochat *et al.* 2006; McKinney 2008).

Several studies have revealed how urbanization can affect vertebrate population dynamics (Chase and Walsh 2006; Glista *et al.* 2008; Delaney *et al.* 2010). In the case of freshwater turtles, roads have been one of the major factors responsible for mortalities, skewed sex ratios and other changes in population structure (Steen and Gibbs 2004; Aresco 2005a; Eskew *et al.* 2010a, b). Nonetheless, suburban areas with high levels of connectivity among habitat patches and increased productivity from urban green spaces (e.g. golf courses) can have abundant and healthy populations of turtles (Rees *et al.* 2009; Roe *et al.* 2011; Guzy *et al.* 2013). Many strategies have been applied to mitigate the impacts of urbanization on turtles, such as the use of under-road culverts and fencing to funnel their movements into the under passages (Dodd *et al.* 2004; Aresco 2005b; Rees *et al.* 2009).

Monitoring of wildlife populations is essential to understand changes in population dynamics through time (Witmer 2005; Marsh and Trenham 2008). Many long-term studies have been successful in detecting population trends, such as in cases of small mammals in Canada (Krebs 1996; Fryxell *et al.* 1998), in addition to detecting declines and estimating demographic parameters in turtles (Stickel 1978; Congdon *et al.* 1994). Despite caveats for the interpretation of short-time series data sets (Fryxell *et al.* 1998), short- to mid-term studies are relevant to pinpoint specific ecological questions (Waide 1991; Schmiegelow *et al.* 1997). Monitoring responses of native species to dynamic threats such as urbanization is key to understanding their persistence in the interface of natural-urban environments (Boal and Mannan 1999; Shochat *et al.* 2006). In addition, interactions with factors such as climate cycles (wet and dry) can be insightful, as these and other environmental fluctuations can introduce additional challenges or opportunities that impact both behavior and population responses (Bowne *et al.* 2006; Roe and Georges 2008; Roe *et al.* 2011).

Chelodina longicollis is an Australian freshwater turtle that inhabits a wide range of water bodies, including natural and developed environments (Kennett *et al.* 2009). The behavior of this turtle is variable and depends on local environments and climate (Roe and Georges 2008). For example, a previous study demonstrated that *C. longicollis* in drought conditions are more vagile and aquatic in the suburbs compared to turtles from an adjacent nature reserve, while turtles in the nature reserve remained inactive in terrestrial aestivation for prolonged periods of time (Rees *et al.* 2009). The species is also more abundant and grows faster in the suburbs, and have more adult turtles in the larger sizes classes than nature reserve populations (Roe *et al.* 2011).

Given our comprehensive understanding of *C. longicollis* ecology in contrasting habitats during drought, where suburban ponds remained flooded and nature reserve ponds dried (Rees *et al.* 2009; Roe *et al.* 2011), we were interested in monitoring the species in the same system following several environmental changes five years later. The first study (Rees *et al.* 2009; Roe *et al.* 2011) was conducted during the early stages of urban development, and the region has since experienced rapid population growth and associated urban infrastructure, including additional roads, houses, and a pest-exclusion fence designed in part to isolate the nature reserve from encroaching suburban threats. Second, climate conditions were appreciably wetter than during the first study. We hypothesize that the effect of such changes could potentially affect turtle behavior and ultimately alter important population vital rates such as survivorship during the time frame. Specifically, we aimed to (1) compare the spatial ecology and behavior of female *C. longicollis* in a suburb and an adjacent nature reserve during a wet period, (2) evaluate the survivorship of female *C. longicollis* between environments, and finally (3) contrast the present results with the previous investigation following changes to the system.

Methods

Study area

This study was undertaken from January 2012 to April 2013 in suburban Gungahlin and in Mulligans Flat Nature Reserve, which is an adjacent reserve, Australian Capital Territory (ACT), Australia. Gungahlin, established in 1975, is a fast growing suburb in Canberra and development continued throughout our study. The Gungahlin suburbs are characterized by large areas of residential, industrial and agricultural development, in addition to elevated road densities and urban green spaces such as sport ovals, golf courses, gardens and suburban parks. There are also several suburban water bodies, including two large reservoirs > 25 ha, smaller golf course and stormwater drainage ponds, and several streams that form the Ginninderra Creek drainage (Rees *et al.* 2009). Adjacent to Gungahlin, there are two connected natural reserves, Mulligans Flat (791 ha) and Goorooyaroo (703 ha), which consist of woodlands, grasslands, several ponds and the upper tributaries of Ginninderra Creek. Both nature reserves are surrounded by urban development and farmlands. For a detailed description of the study sites, see Rees *et al.* (2009) and Roe *et al.* (2011).

In 2009, a predator-proof fence was established in Mulligans Flat Nature Reserve to allow the managed re-introduction of locally extinct species of animals and consequently protect native species against invasive and pest species such as foxes, hares, rabbits, feral cats and dogs (Shorthouse *et al.* 2012). The fence is 11.5 Km in length and encloses 485 ha of the reserve (Shorthouse *et al.* 2012).

The climate of the ACT is temperate, with mean monthly maximum air temperature ranging from 11°C in July to a peak 27°C in January and February, and a mean monthly minimum air temperature ranging from 0°C to 13°C in the same months (Palmer-Allen *et al.* 1991). Although the mean annual rainfall is 600 mm (Palmer-Allen *et al.* 1991), the weather in Australia is unpredictable, with long periods of drought, the last known as the “Millennium drought”, which occurred during 2001-2009, with a yearly below median rainfall, mainly influenced by El Niño events (483 mm/year; van Dijk *et al.* 2013). In contrast, there are periods of elevated rainfall and flooding, influenced by La Niña events, such as occurred in 2010-2011 and 2011-2012 (BOM 2012; Letnic *et al.*

2013). Our study took place during a La Niña period, with elevated rainfall, indicating a 965 mm of rainfall from Jan2012 to Apr2013 (Australian Bureau of Meteorology).

Water levels and urban growth

To describe fluctuations in water depth in the study sites, we measured maximum water depth monthly from January 2012 to April 2013 in four ponds each within the suburbs and Mulligans Flat Nature Reserve. We accessed the growth of the Gungahlin suburbs in terms of human population and car traffic volume for comparisons with the previous study conducted during 2006-2007 (Rees *et al.* 2009). Human population growth was compared using Census data in 2006 and 2012 (Australian Bureau of Statistics) and other impacts from the five new suburbs of the Gungahlin District (Amaroo, Bonner, Forde, Gungahlin, and Ngunnawal) that surround the study sites. We accessed the car traffic volume comparing information from a major road, Horse Park Drive, which crosses our study sites and give a reliable measure on how traffic volume changed through time. Data was obtained from Territory and Municipal Services, comparing road traffic in Horse Park Drive as a volume of cars per day in July 2007 and August 2011. This data was collected with the use of portable sensors (pneumatic tubes) attached to the road.

Capture and radio-transmitter attachment

Turtles were captured using traps baited with sardines and cow liver, from five ponds in the nature reserve and four in the suburbs. We only selected female turtles for this study, as previous information on movements differences between males and females was already available for this area (Rees *et al.* 2009), and females are most important for the recruitment and survivorship of the population (Congdon *et al.* 1993). Radiotransmitters were initially attached to 40 females divided equally between the nature reserve and suburban sites. If a turtle died during the study, the radiotransmitter was attached to another female from the same study site. We used transmitters manufactured by Holohil Systems Ltd. (Carp, Ontario, Canada) (Models: RI-2B and AI-2F, 14 - 21g). For details on the transmitter attachment protocol, see Doody *et al.* (2009). Initial carapace length and mass for nature reserve females were 199.8 ± 19 mm (mean ± standard deviation) and 909.9 ± 229.9 g, respectively, and for suburb females were 203.9 ± 20 mm and 926.7 ± 242.4 g, respectively. Transmitters were 1.1-3.75% of the turtle's initial body mass.

Radio-telemetry data collection

We tracked turtles once per week during the active season (September to April), and once per month during the inactive period (May to August). Whenever possible, location of individuals were recorded by holding a GPS (GPS III Plus, Garmin Corp., Olathe, Kansas) over the animal; otherwise, locations were performed by triangulation and plotted on an aerial photograph. We used ArcGIS (version 9.3.1: ESRI, 2009) to plot locations on habitat maps previously developed by Rees *et al.* (2009), with corrections using a 2012 aerial photograph.

We calculated several movement behavior variables to compare turtles from natural *versus* suburban habitats, in addition to turtles inhabiting small size *versus* large size ponds in both study sites. Home range was estimated by the minimum convex polygon (MCP) method, which describes the size of the area traversed by each turtle. The criteria used to include individual turtles for the home range analysis were to have a minimum of 30 locations during the active season (Sep - Apr) (Plummer and Mills 2000; Donaldson and Echternacht 2005), as MCP home ranges estimates are sensitive to sample size (Seaman *et al.* 1999). Linear range length was calculated as the Euclidean distance between the two most widely spaced locations. Movement distance was also calculated, measured as the sum of Euclidean distances among sequential radio-locations for each turtle. In addition, we calculated the number of different wetlands a turtle used, and the number of times a turtle moved between these wetlands, both metrics representing an index of inter-patch movement extent and frequency (Roe and Georges 2007; Rees *et al.* 2009). We also assessed if turtles were in an aquatic or terrestrial habitat at each location, using a metric to calculate terrestrial behavior - terrestrial habitat proportional use, which was the proportion of all locations that a turtle was found in terrestrial habitat. Movement behavior was estimated using Hawth's Tools extension for ArcGIS (version 9.3.1: ESRI 2009).

Data analysis

Statistical analysis were performed with SPSS (Version 21) and the program MARK version 7.1 (White and Burnham, 1999). The assumptions of normality and homogeneity of variances were checked by analysis of residuals and when data failed to meet these assumptions, data were transformed to approximate normal distributions and equal variances; otherwise non-parametric tests were used. Statistical significance was accepted at the α= 0.05 level unless specified otherwise.

To compare MCP, range length, distance moved, number of wetlands used, and proportion of time spent in terrestrial habitats between nature reserve (N= 19) and suburban areas (N= 13) turtles, we used an independent-samples T-test. We log (ln) transformed MCP, and proportion of terrestrial locations, to better meet the assumptions. We used a Mann-Whitney test to compare inter-wetland movement of turtles from natural and suburban sites. We did not consider the use of analysis of covariance for the comparisons above as carapace length was similar between turtles from nature reserve and suburbs (Mann-Whitney U test: U=243.5, z= -0.76, df= 47, p=0.44).

For comparisons of movements between turtles from small and large ponds in the nature reserve and suburbs, we initially averaged the size of wetlands used by each individual, and then we used this mean value as our predictor variable. We used linear regressions to evaluate the influence of wetland size used by turtles on three movement metrics: number of wetlands used, number of inter-wetland movements, and MCP in each study area (response variables). The response variables were log (ln) transformed in both analysis to better meet the assumptions. The Dunn-Sidak adjusted α level for statistical significance for this groups of tests was $\alpha \leq 0.017$. We calculated road density around the suburb ponds and correlated it with turtle deaths on roads to help in identifying hotspots of turtle mortality. We initially created 700m buffers around the suburban ponds with ArcGIS (version 9.3.1: ESRI 2009). This distance was based on typical movement distances of *C. longicollis* determined from previous studies in the region (Rees *et al.* 2009; Roe and Georges 2007; Roe *et al.* 2009). Then we calculated road density (km of road/km^2) within each buffer.

To assess if turtle movements were associated with environmental variables we performed multiple linear regressions, using weekly movements from each turtle (response variable), and location (nature reserve or suburb), season (Summer 2012, Fall 2012, Winter 2012, Spring 2012, Summer 2013, Fall 2013), daily maximum tempeature (°C), and rainfall (mm), as the predictor variables. We used turtles' weekly movements as the linear distance representing the movement between locations each week. We then used the mean value of daily maximum temperature per week and the rainfall accumulated during the week period. Weekly movements were log (ln) transformed to better meet assumptions. For this analysis, we used the locations of 20 females in the nature reserve, and 26 females in the suburbs.

We used known fate models in the program MARK (White and Burnham, 1999) to evalute differences in survivorship analysis between adult female turtles from nature and suburban sites. Time periods when radio-signals could not be detected (i.e. transmitter failure or undetected long-distance movements) were censored from the analysis. If a turtle died during the study, we fitted the transmitter in another turtle from the same population and entered the data as “staggered” in its the capture history (Cooch and White 2014). Akaike information criterion (AIC) were used to rank candidate models; if competing models had AIC values of < 2.0, they were considered as having some support. Maximum likelihood survival probablities were estimated over monthly intervals. Annual survival probability was estimated by using the monthly probability from the real function parameters and raised to a 12 (months) exponent. We started with a fully-saturated model in which survival probability was dependent on site, time, and their interaction, then we fitted a series of reduced-parameters models. We did not consider carapace length of turtles as a covariate as there were no difference in carapace length between sites (Mann-Whitney U test: U=243.5, z= -0.76, df= 47, p=0.44).

Results

Water levels

Water levels fluctuated more in nature reserve ponds than in the suburbs (Fig. 3.1). Nonetheless, ponds from neither site experienced expressive drops in water level, and all wetlands remained flooded throughout the study period.

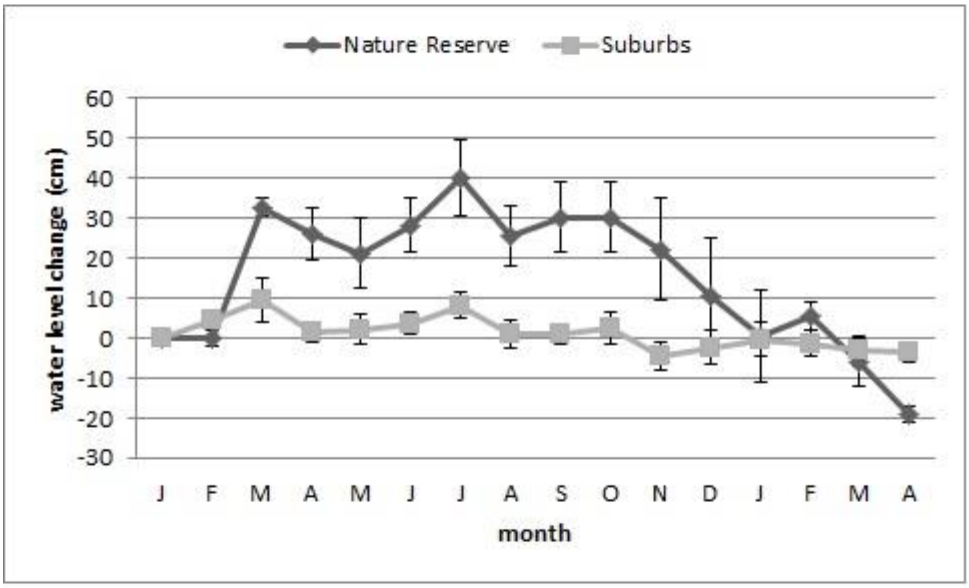

Figure 3.1. Water level fluctuation relative to the beginning of the study (January 2012) in nature reserve and suburbans ponds, Australian Capital Territory, Australia. Values are mean ± 1 standard error.

Movements

We radio-tracked turtles for an average of 262 ± 18 (7- 364) days, and gathered an average of 37 ± 3 (1 – 52) locations for each turtle. There was no difference between turtles from naturereserve and suburban turtles in MCP size estimates (*t* (30) = 0.34, p = 0.74), range length (*t* (30) = - 0.39, p = 0.70), number of wetlands used (*t* (30) = 0.98, p = 0.33), proportion of terrestrial locations (*t* (4) = 1.52, p = 0.20) or inter-wetland movement frequency (Mann-Whitney U test: U = 107.5, Z = - 0.64, df = 31, p = 0.52) (Table 3.1). However we observed differences in distances moved, with suburban turtles moving more than natural reserve turtles (*t* (30) = -2.84, p = 0.008) (Table 3.1). No radiotracked turtles were observed in prolonged aestivation on land in any of the study sites. The few observations of turtles in terrestrial habitats were walking along the inside and outside of the predator-proof fence and two individuals in the nature reserve that shortly aestivated in the grassland close to the inside of the predator-proof fence (7.6 m and 10 m away), one for no longer than seven days and the other for less than 14 days, and then returned to the pond.

When comparing turtle's movements from small and large ponds in the nature reserve and suburbs, we observed a similar pattern. The size of ponds turtles used did not influence home range (MCP) (Nature reserve: $F_{1, 17} = 0.09$, $r^2 = 0.09$, $p = 0.77$; Suburb: $F_{1, 11} = 0.03$, $r^2 = 0.003$, $p = 0.87$) or number of inter-wetland movements (Nature reserve: $F_{1, 13} = 2.70$, $r^2 = 0.17$, $p = 0.12$; Suburb: $F_{1, 4} = 5.94$, $r^2 = 0.59$, $p = 0.07$) in any of the sites. However, turtles from smaller ponds used more wetlands than turtles from larger ponds in both sites (Nature reserve: $F_{1, 17} = 8.93$, $r^2 = 0.35$, $p = 0.008$, Predictor variable- Area of wetland: Beta = - 0.59, $p = 0.008$; Suburb: $F_{1, 11} = 10.11$, $r^2 = 0.48$, $p = 0.009$, Predictor variable- Area of wetland: Beta = - 0.69, $p = 0.009$) (Fig. 3.2). In addition, we observed that radiotracked turtles that died on roads in the suburbs where mainly inhabiting smaller ponds, but road density was similar around both large size and small size ponds (Fig. 3.3, Table 3.2).

Table 3.1. Spatial ecology and movements of female *Chelodina longicollis* in nature reserve and suburban habitats comparing a previous and the present study in Gungahlin, Australian Capital Territory, Australia. Values expressed in Mean ± SE (range).

		MCP[b] (ha)	Range length (Km)	Distance moved (Km)	Wetland used (n)	Inter-wetland movements (n)	Proportion of terrestrial locations
Previous study [a] (Drought)	Nature reserve	8.7 ± 2.2 (0.7-31.8)	0.6 ± 0.2 (0.2-1.9)	1.5 ± 0.2 (0.7-2.9)	2.3 ± 0.3 (1-4)	1.5 ± 0.4 (0-4)	0.28 ± 0.76* (0-0.77)
	Suburb	14.2 ± 4.7 (0.3-37.2)	0.8 ± 0.2 (0.1-1.9)	3.0 ± 0.6 * (0.7-6.6)	2.3 ± 0.4 (1-5)	1.9 ± 0.7 (0-6)	0 ± 0
Present study (Wet)	Nature reserve	17.2 ± 4.2 (0.3-70.6)	0.8 ± 0.1 (0.1-1.5)	3.7 ± 0.3 (1.2-5.5)	1.9 ± 0.1 (1-3)	1.3 ± 0.2 (0-3)	0.01 ± 0.004 (0-0.06)
	Suburb	11.9 ± 3.7 (1.6-53.5)	0.9 ± 0.1 (0.4-2.1)	4.9 ± 0.3* (3.0-6.4)	1.6 ± 0.2 (1-3)	1.7 ± 0.7 (0-7)	0.001 ± 0.01 (0-0.02)

[a] Rees *et al.* 2009, [b] Minimum convex polygon, * indicate difference between groups during each study period

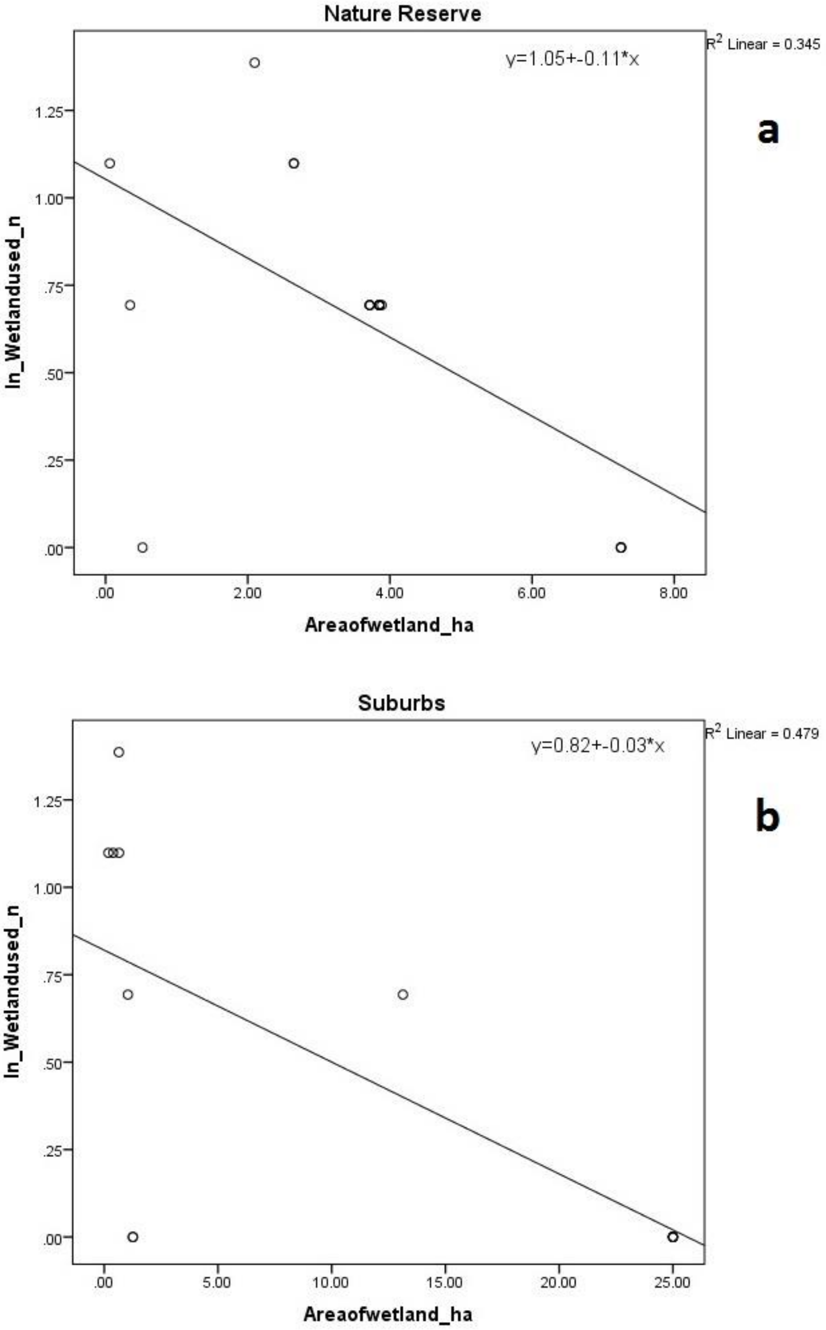

Figure 3.2. Relationship between response variable (number of wetlands used: ln_Wetlandused_n) and the predictor variable (size of wetlands used: Areaofwetland_ha) in linear regression analysis in *Chelodina longicollis* inhabiting nature reserve (a) and suburban (b) ponds in Gungahlin, Australian Capital Territory, Australia.

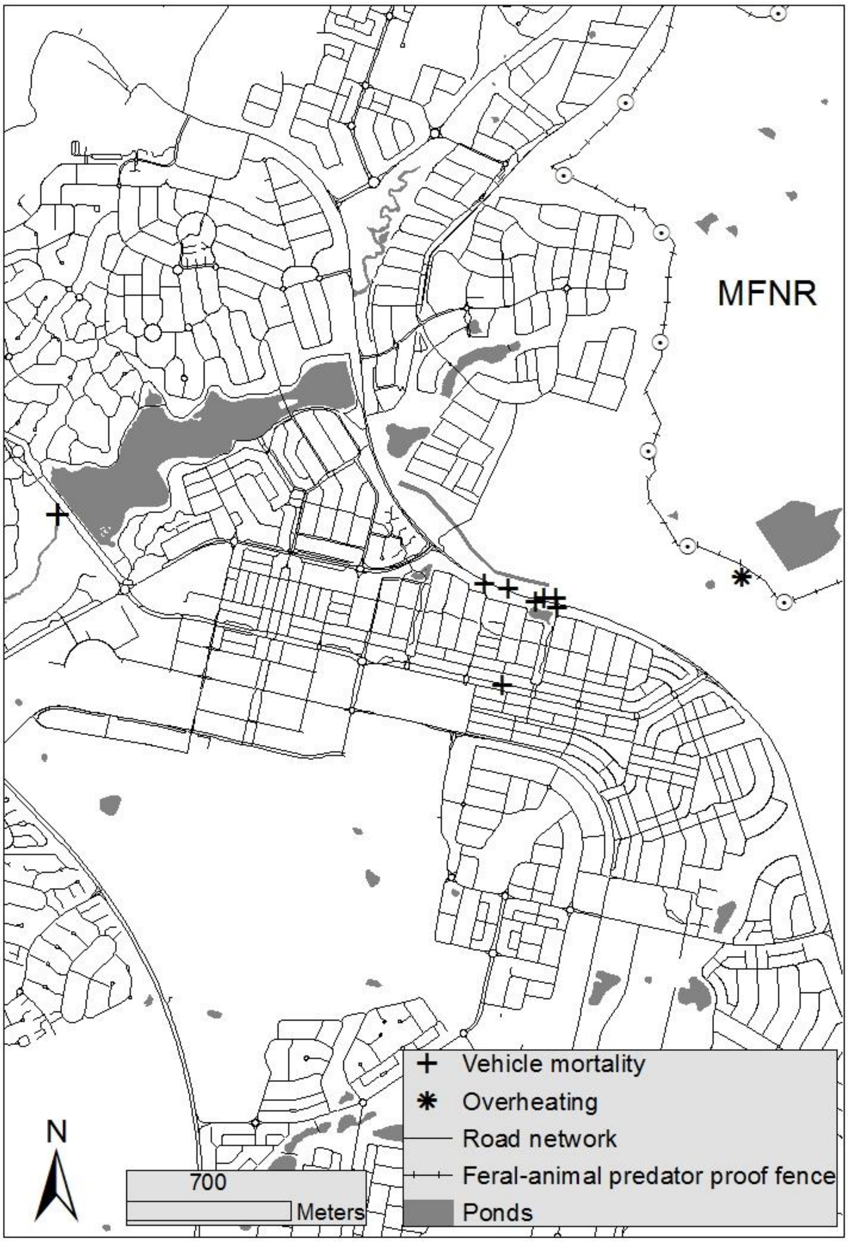

Figure 3.3. Deaths of female *Chelodina longicollis* monitored by radio-telemetry in the Gungahlin suburb during wet period, Australian Capital Territory, Australia (MFNR - Mulligans Flat Nature Reserve).

Weekly movements of turtles were positively correlated with daily maximum temperature and rainfall, but these explain only 4% of the variation in turtle movement ($F_{4, 1738} = 18.45$, $r^2 = 0.04$, $p < 0.001$) (Predictor variables: daily maximum temperature: Beta = 0.19, $p < 0.001$; rainfall: Beta = 0.08, $p < 0.001$). Location (Beta = 0.02, $p = 0.42$) and season (Beta = 0.04, $p = 0.07$) had no influence on the movements of turtles.

Survivorship

We found little evidence that survival probability varied over time (Table 3.3). The model with the most support included only site variation in survivorship, with no support for time-dependent models (Table 3.3). Estimated survivorship probabilities over the duration of the study were 1.00 ± 0.0 for nature reserve turtles and 0.59 ± 0.1 (0.38 – 0.77) for suburban turtles, which equates to an annual survivorship of 0.67 ± 0.01 (0.46 – 0.81) for suburban turtles. Of the nine mortalities for suburban turtles, eight were killed by vehicles and one was found dead along the predator-proof fence, presumably from overheating, when trying to get into the nature reserve (Fig. 3.3). Most of the turtle mortalities caused by vehicle collisions (seven of eight) occurred in the vicinity of two small ponds in the suburbs (Fig. 3.3, Table 3.2). These small ponds are located about 35 meters away from a major road (Fig. 3.3). Although there is an under-road culvert, turtles do not always use it while attempting to reach wetlands in the other side of the road. The other vehicle mortality occurred while a turtle left a golf course pond and was attempting to reach a large reservoir in the suburb (Fig. 3.3, Table 3.2).

Table 3.2. Road mortality and pond characteristics of radiotracked female *Chelodina longicollis* in Gungahlin suburbs, Australian Capital Territory, Australia.

	Large ponds		Small ponds	
	Yerabi	Golf	Ford canal	Gung.8
Turtle vehicular collision (n)	0	1	2	5
Pond area (ha)	25	1.26	0.62	0.30
Road density (km of road/km^2)	19.94	15.68	18.39	16.82

Table 3.3. Models of survivorship probability (*S*) of female *Chelodina longicollis* between sites (site) over monthly time intervals (time), Australian Capital Territory, Australia.

Model	AICc	ΔAICc	Weight	Model Likelihood	N	Deviance
S (site)	83.21	0.00	0.996	1.000	2	19.20
S (.)	94.72	11.52	0.003	0.003	1	32.73
S (time)	106.66	23.45	0.000	0.000	16	13.70
S (time x site)	127.87	44.66	0.000	0.000	32	0.00

Discussion

Our investigation demonstrated the value of a repeated longitudinal study for turtle populations, where we observed their responses to both natural (rainfall) and anthropogenic (urbanization) environmental changes. The main findings can be summarized as follows: (1) changes in the underlying environmental challenges/threats can occur in the short term, which can significantly influence important population vital rates, such as survival, in turtles. This is of broader conservation impact because urban environments are rapidly growing worldwide, presenting accelerating challenges to suburban wildlife, some of which might not be able to cope and persist; (2) turtle behaviors are influenced by environmental conditions in potentially interactive relationships, as the behavior of suburban turtles was largely similar in drought and wet periods, while several critical aspects of behavior changed dramatically for nature reserve turtles according to drought/wet cycles; and (3) turtles inhabiting small ponds in both study sites use more wetlands than turtles from large ponds, which means they make more overland movements at increased risk of vehicular collisions.

We observed significant lower annual survivorship for suburban female turtles compared to their nature reserve counterparts, a finding in contrast with a previous study in our system during drought, where survival was similar between sites (Rees *et al.* 2009). Although survivorship estimates in the previous study included males, sex was not a significant predictor variable in models (Rees *et al.* 2009). Over the five-year period between studies, annual survivorship of suburban turtles dropped from 0.876 (Rees *et al.* 2009) to 0.67, a reduction of 20%. It is possible that differences in rainfall could explain such increased mortality, as the previous study occurred during drought (study period rainfall: 649 mm, Australian Bureau of Meteorology) (Rees *et al.* 2009; Roe *et al.* 2011), while the present study occurred during a relatively wet period (study period rainfall: 965 mm, Australian Bureau of Meteorology). It has been demonstrated that *Chelodina longicollis* movements and overland migration increase during rainfall (Roe and Georges 2008a; Roe *et al.* 2008), potentially exposing turtles to vehicular mortality and other threats. Indeed, female turtles moved longer total distances in the nature reserve and suburbs during wet period compared to drought (Table 3.1), but the two metrics that better reflect frequency of overland movements (number of wetlands used and frequency of inter-wetland movements) were similar between wet and dry conditions (Table 3.1). It is also possible that terrestrial nesting excursions were more frequent during wet conditions, a behavior that exposes female turtles to increased risk of mortality on roads (Steen and Gibbs 2004; Aresco 2005a; Steen *et al.* 2006). However, we did not track turtles with high enough frequency to provide details of such overland movements.

An alternative explanation for the drop in survivorship for suburban turtles between studies is rapid human population growth and associated infrastructure in the region, which then increased the road traffic around our study sites. Human population increased 79.2% from 2006 to 2011 in Gungahlin suburbs of Amaroo, Bonner, Forde, Gungahlin, and Ngunnawal (2006: 13.381 people; 2011: 23.985 people) (Australian Bureau of Statistics). Additionally, traffic volume on Horse Park Drive, a major road bisecting our study area, increased 76% from 2007 to 2011 (July 2007: 3086 cars/day; August 2011: 5435 cars/day) (Territory and Municipal Services). Only one radiotracked turtle was killed by a vehicle in 2006-2007 (Rees *et al.* 2009), compared to eight individuals killed by vehicles in the present study. We propose that the probability of being killed during road crossings likely increased between study periods. Numerous studies have modeled or demonstrated increased risk of vertebrate mortality as traffic volumes increase (Hels and Buchwald

2001; Mazerolle 2004; Aresco 2005b). The survival estimates in suburban turtles in the present study are lower than the normal range in *C. longicollis* elsewhere (Roe *et al.* 2009), and when compared to other freshwater turtles (Shine and Iverson 1995).

Despite the evidence that freshwater turtles are at high risk of road mortality (Gibbs and Shriver 2002; Marchand and Litvaitis 2004; Aresco 2005a), and can have low survivorship estimates in urbanized landscapes (Eskew *et al.* 2010a, b), it was previously hypothesized that *C. longicollis* low mortality rates observed in the earlier study in our system were in part owing to the availability of vegetated drainage lines and under-road "box" culverts that facilitated turtle movements in the suburb while avoiding threats (Rees *et al.* 2009). However, given the new evidence, clearly turtles in our system do not always use under-road culverts even when available and are thus susceptible to road mortality. In addition, females could be in search of nesting areas and increase the risk of vehicular collision (Aresco 2005a). We demonstrated that turtles inhabiting smaller ponds used more wetlands than turtles from large ponds, requiring them to move overland to access different wetlands and resources, increasing risks of vehicular collisions. Indeed, most road mortalities occurred for turtles inhabiting smaller ponds, despite similar road densities surrounding ponds of all sizes in the suburban study site (Table 3.2). Such results indicate the presence of hotspots of mortalities for turtles within suburban areas. The identification of hotspots of turtle mortality has been mainly focused on highways and open roads (Langen *et al.* 2009; Cureton and Deaton 2012; Crawford *et al.* 2014), but few studies have focused on peri-urban sites for vertebrates in general (Ramp *et al.* 2006; Wotherspoon and Burgin 2011), demonstrating the relevance of identifying hotspots within the city. Although the ponds in the suburb are in the same drainage and seem to be all interconnected in the large scale, they could represent a case of pseudo replication.

However, in the small scale, the suburb ponds are disconnected from each other by roads and urban development, consequently turtles would need to move overland to reach different wetlands. Despite the presence of culverts in some regions, water levels are usually low and consequently ponds from each side of the road are disconnected as well.

The importance of connectivity of greenspaces in suburban areas has been highlighted for predicting species richness and species-specific occupancy in turtles (Guzy *et al.* 2013). Connectivity is also important for influencing inter-pond movements and occupancy in freshwater turtles in an agricultural landscape (Bowne *et al.* 2006). Land managers should consider the ecology of species when planning new areas of development and we suggest that large ponds and aquatic connectivity among suburban ponds should be the option over smaller and isolated ponds to avoid mortality of vagile vertebrate species within the suburbs.

In the present study, nature reserve turtles could not move into the suburbs because of the predator-proof fence, a behavior of critical importance in response to drought in the previous investigation (Rees *et al.* 2009). Turtles inside the nature reserve enclosure are now protected against fox depredation, potentially contributing to the turtle's high survivorship in this environment. However, we observed significant indirect mortality of freshwater turtles, especially in the outside of the fence (98 turtle deaths in 16 months of monitoring; Ferronato *et al.* 2014), including one of the suburban turtles in our radiotracked sample that died of apparent overheating outside of the fence. Consequently, not only do roads present a challenge for turtles living in natural-urban gradients, but in some cases fences may block their migratory routes.

In our longitudinal study, we were also able to examine how turtle behavior is influenced by environmental factors, such as rainfall and if wetlands are dry or filled up, and how it can possibly interact with site-specific conditions, particularly urbanization. The wet period during the present study released nature reserve turtles from dormancy, as most individuals entered prolonged aestivation (up to 10 months) in terrestrial habitats when the reserve ponds dried during 2006-2007 (Rees *et al.* 2009). When nature reserve ponds remained flooded during the present study period, turtles did not aestivate for extended periods on land. The only terrestrial observations were for relatively short periods (less than 14 days) when turtle's movements were interrupted by the fence as they attempted travel to wetlands outside of the predator-proof enclosure (See Results). Additionally, turtles in the nature reserve moved longer distances and used larger areas of habitat (MCP) when compared to drought (Table 3.1), although rainfall was only partially correlated to turtle movements in the present study. Interestingly, suburban turtles showed similar behaviors regardless of the dry/wet cycles, as turtles did not aestivate on land during drought or wet conditions, instead remaining active and vagile through the suburban landscape (Table 3.1). This is possibly a result of the hydrological stability of suburban ponds owing to increased runoff, irrigation inputs, and intentional manipulation (Rees *et al.* 2009). The dissimilarity in behavior between wet and dry cycles, at least in natural habitats, reinforces the idea that terrestrial aestivation in *C. longicollis* is a behaviorally plastic response influenced by wetland drying and the proximity to other permanent wetlands (Roe and Georges 2008b). In addition to the changing behavioral dynamic, wetter times coupled with increased road density and traffic also brought upon higher mortality from vehicles in the suburban population, at least on localized scales. The findings of reduced survivorship of suburban turtles compared to nature reserve counterparts and the identification of hotspots of turtle's mortality on roads are valuable for conservationists and managers to implement mitigation on local scales.

Wildlife inhabiting urban areas face the challenge of dealing with patchy habitats, low connectivity and increased risks of mortality (Blair and Launer 1997; McKinney 2002; Aresco 2005a; Steen *et al.* 2006). Although many studies have provided guidance for managers to protect vertebrates against threats such as roads (Yanes *et al.* 1995; Clevenger *et al.* 2001; Dodd *et al.* 2004; Aresco 2005b), continued monitoring is essential to understand responses of animals to urban challenges in space and over time (Cosentino *et al.* 2010). Many cities worldwide, especially in developing countries, will likely continue to grow in human population and associated infrastructure, such as roads and traffic (World Resources Institute *et al.* 1996; Gakenheimer 1999; Schafer and Victor 2000). Managers and conservationists need to be alert to how such changes can affect native wildlife. We were able to demonstrate that short- to mid-term changes in suburban conditions, such as increase in traffic, could lead to a decrease in survivorship of a vertebrate species. Consequently, mitigations need to be applied to help the persistence of turtles in suburban areas, such as the implementation of connectivity in greenspaces (Guzy *et al.* 2013).

Chapter 4

Responses of an Australian freshwater turtle to drought-flood cycles along a natural to urban gradient

The manuscript will be submitted for publication in the journal **Ecological Applications** as: Ferronato, B.O., Roe, J.H., Georges, A. Responses of an Australian freshwater turtle to drought-flood cycles along a natural to urban gradient. Presented as submitted with minor formatting changes.

Abstract: Urban areas provide habitat for numerous native species, but life in the city presents many challenges. We investigated demography, growth rates, movements and reproduction of a semi-aquatic freshwater turtle, *Chelodina longicollis,* along a natural to urban gradient during a period of relatively high rainfall, and compared our results to a previous study in the same system during drought (Roe *et al.* 2011). Between the present and previous study, urbanization increased dramatically and a pest-exclusion fence was constructed to mitigate against encroaching suburban hazards. Turtles grew at similar rates, had similar abundances and sex ratios, and similar reproductive output across the gradient from urban to non-urban sites during the wet period. Despite increasing urbanization, recruitment occurred at all sites and survivorship estimates were similar among sites. Turtles moved among wetlands at high rates and over long distances (6 km), underscoring the importance of movements in suburban landscapes. Such movements are also threatened by the pest-fencing, preventing dispersal in response to drought. When compared with earlier studies (Rees *et al.* 2009, Roe *et al.* 2011). of the same system during drought, where nature reserve turtles grew less and were less abundant than suburban turtles, in addition to exhibit aestivation on land for extended periods in response to wetland drying, but not in suburban turtles as suburban ponds retained water, our

current results underscore the strong influence of rainfall on population dynamics for *C. longicollis* and the resilience of this species to changes brought about by urbanization. Further monitoring is required to understand the longer-term population responses of long-lived species to drought-flood cycles within natural-urban gradients.

Introduction

Urbanization refers to the complex interaction of different processes that transform landscapes formed by rural life styles into urban ones (Antrop 2000, 2004; Pacione 2001). Growth of cities and the associated urban sprawl encroaches on natural habitats with negative consequences for many native species (Gakenheimer 1999; McKinney 2002, 2008; Pauchard *et al.* 2006) as a result of habitat loss, chronic stress, disease, interactions with invasive or subsidised competitors and predators, environmental contamination, and direct mortality from roads and other human activities (Chase and Walsh 2006; Bradley and Altizer 2007; McKinney 2008). Species richness tends to diminish from the margins to the urban core, where primarily generalist species continue to persist (McKinney 2002, 2008). An improved understanding of ecosystem dynamics is needed to mitigate possible impacts on wildlife if biodiversity in the suburbs is to be maximized (Grimm *et al.* 2000; Ditchkoff *et al.* 2006).

Urban waterways can provide suitable habitat for some freshwater turtles (Gibbons 1967; Lindeman 1996; Marchand and Litvaits 2004; Plummer *et al.* 2008), while others may be adversely affected by the habitat alteration accompanying urbanization (Gibbs and Shriver 2002; Marchand *et al.* 2002; DeCatanzaro and Chow-Fraser 2010). Population declines have been attributed to road mortality, which also leads to male-bias owing to female mortality during nesting excursions (Gibbs and Shriver 2002; Marchand and Litvaits 2004; Aresco 2005). Recruitment is often lower as a result of high rates of nest and juvenile depredation from native or introduced predators (Mitchell and Klemens 2000; Marchand *et al.* 2002) and reduced availability of suitable nesting sites (Spinks *et al.* 2003). In addition, competition with invasive species is a growing threat in urban areas (Cadi and Joly 2004; Thomson *et al.* 2010). For some turtle species, declines may be offset by increased productivity of urban waterways, leading to faster growth, higher fecundity, and ultimately higher population abundances compared to natural populations (Gibbons 1967; Brown *et al.* 1994; Lindeman 1996; Souza and Abe 2000; Roe *et al.* 2011).

The eastern long-necked turtle (*Chelodina longicollis*) is a generalist and opportunistic species with a marked propensity for overland movements (Roe and Georges 2008a; Rees *et al.* 2009), enabling it to exploit a wide range of aquatic habitats, including ephemeral and permanent wetlands (Kennett and Georges 1990; Roe and Georges 2008a,b; Roe *et al.* 2009). The species can be found in rivers, lakes, farm dams (reviewed by Kennett *et al.* 2009), and in urban and suburban waterways (Burgin and Ryan 2008; Rees *et al.* 2009; Roe *et al.* 2011; Stokeld *et al.* 2014). Suburban *C. longicollis* can also grow faster and become more abundant than their counterparts in natural areas (Roe *et al.* 2011). However, the mechanisms involved in such demographic responses in suburban landscapes are not completely understood and may depend upon a suite of interacting factors, including climate (Rees *et al.* 2009; Roe *et al.* 2011) and interactions with exotic predators (Spencer and Thompson 2005; Spencer *et al.* 2006). In addition, most studies examining responses of *C. longicollis* to urbanization are limited to short-term (< 2 years) snapshots (Rees *et al.* 2009; Roe *et al.* 2011; Stokeld *et al.* 2014), which can lead to an incomplete understanding of responses to urbanization. Longer-term studies have proven essential in understanding population dynamics of long-lived animals such as turtles (Roe and Georges 2008a,b).

Here we report attributes of the population biology, including demography, growth rates, movements and reproduction, of *C. longicollis* along a natural to urban gradient during a period of high rainfall following from earlier studies in the same system during a period of low rainfall (Rees *et al.* 2009; Roe *et al.* 2011). In conducting a longitudinal study, we aimed to examine how turtles responded to three changes in the system with potential importance for population regulation, including increased rainfall, expanding urbanization, and the implementation of a barrier fence. We hypothesize that these changes in the system will influence ecological and demographic responses in *C. longicollis*. Such long-term studies are especially relevant to monitor the impacts of urbanization and other interacting threats for turtles given their life history traits (e.g., long lifespans, delayed sexual maturity) that make populations sensitive to even small reductions in adult survivorship (Congdon *et al.* 1993, 1994).

Methods

Study area

From October 2011 to March 2014, we studied turtle populations from 14 water bodies distributed along an urban gradient (nature reserve, rural and suburb) in the Gungahlin region of the Australian Capital Territory (ACT), south-eastern Australia (Fig. 4.1). The natural site was Mulligans Flat Nature Reserve, 791 ha of woodlands, grasslands, several ponds and the upper tributaries of Ginninderra Creek. In June 2009, a predator-proof barrier fence was erected, as part of a restoration project, enclosing 485 ha of the reserve to isolate it from encroaching urbanization, exclude invasive species, and allow reintroduction of locally extinct native species (Manning *et al.* 2011; Shorthouse *et al.* 2012). The nature reserve site was defined here as having a low degree of anthropogenic impact isolated by the fence enclosure. We sampled turtles in five wetlands within the enclosure.

Five wetlands were also sampled in the rural landscape including two wetlands in the Ginninderra Experimental Station and three wetlands in Goorooyaroo Nature Park. The Ginninderra Experimental Station consists of areas with native grasses and eucalypts, in addition of areas with crops and pastures (Webster and Butler 1976). Goorooyaroo is adjacent to Mulligans Flat Nature Reserve, with similar vegetation characteristics, but is not enclosed by the barrier fence. The rural site was defined as having intermediate degree of anthropogenic impact including agriculture and low-level urban development, and exposure to invasive predators such as the European fox.

Finally, four wetlands were sampled from the suburban site located in the central Gungahlin suburb, including a large reservoir, a golf course pond, a canal, and a storm water drainage pond. This area is subject to industrial and residential development, including high road densities and managed suburban green spaces such as golf courses, suburban parks, gardens and sport ovals (Rees *et al.* 2009; Roe *et al.* 2011). This site was defined as having high degree of anthropogenic impact, including urbanization and exposure to invasive predators.

The climate of the ACT is temperate, with a mean annual rainfall of 600 mm (Palmer-Allen *et al.* 1991). Rainfall in southeast Australia is highly variable, with long periods of drought punctuated by flood. The most recent drought occurred from 2001-2009, with a yearly below median rainfall of 483 mm/yr, mainly influenced by El Niño

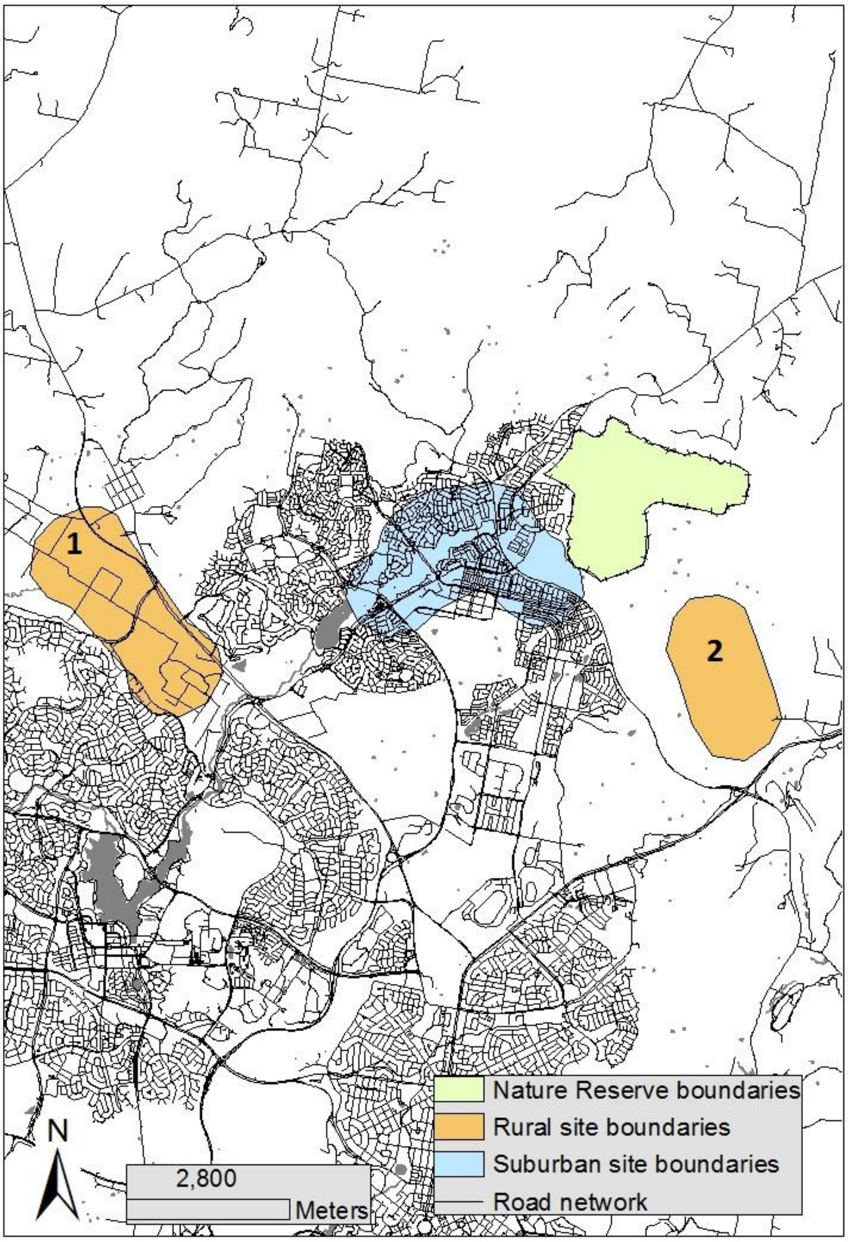

Figure 4.1. Nature reserve, rural and suburban study sites in Gungahlin, northern Canberra, Australian Capital Territory. Study sites were defined by drawing 700 m polygons around the ponds turtles were trapped and then joining the polygons to delimit each site. The polygons in the nature reserve were expanded to delimit the area protected by pest-fencing. Number 1 denotes the Ginnindera Experimental Station and number 2 the Goorooyaroo Nature Park, both part of the rural sites.

events (van Dijk *et al.* 2013). There are also periods of elevated rainfall, influenced by La Niña events (Beard *et al.* 2011). The majority of our study coincided with a La Niña period, with annual rainfall of 694 mm and 534 mm in 2012 and 2013, respectively (Canberra Airport weather station, Australian Bureau of Meteorology).

Trapping and marking

Turtles were captured using traps baited with sardines and cow liver once per month (five consecutive days of trapping per month) from October 2011 to March 2014, excluding months when turtles are inactive (April – August). Our sampling design consisted of ponds that were sampled monthly to accurately describe turtles' reproductive biology (two ponds each in the nature reserve, rural, and suburb sites) hereafter referred to as fixed sites. Additional ponds were sampled only twice a year in order to boost sample sizes for other demographic responses (three ponds each in the nature reserve and rural sites, and two in the suburb site), referred to hereafter as occasional sites. We used two to six traps per pond depending on pond size. We marked captured turtles with unique codes by notching the shell (Kennett and Georges, 1990), and measured maximum straight-line carapace length (CL), carapace width (CW), midline plastron length (PL), and plastron width (PW) with callipers (± 0.1mm) and body mass with a scale (± 5 g). Turtles with a CL < 145 mm were considered juveniles; those for which CL > 145 mm were classified as males or females on the basis of external morphological features (see Kennett and Georges 1990). All turtles were released at their point of capture.

Anthropogenic impact

Anthropogenic impact was measured by calculating road density (km of road/km^2) within 700 m of each of the 14 ponds using ArcGIS (version 9.3.1: ESRI 2009). This distance was based on typical movement distances of *C. longicollis* determined from previous studies in the region (Rees *et al.* 2009; Roe *et al.* 2009). If the buffer encompassed areas within the predator-proof fence, the buffer was rearranged following the fence line, as the fence completely impedes turtle movements (Ferronato *et al.* 2014).

Primary and secondary productivity

We used two techniques to measure primary productivity. First, we measured total phosphorus and nitrogen (TP and TN; ~ 0.2 L) from water samples in each pond, once per month from December 2012 to February 2013 as surrogate of productivity. Water samples were kept on ice in an insulated container during transportation to the lab and analysed using oxidation with $K_2S_2O_8$ and low-pressure microwave digestion (see Maher *et al.* 2002). We also measured primary productivity by assessing the area of algal growth on turtles' carapace. Epiphytic algae are important sources of primary productivity in lakes (Cattaneo and Kalff 1980; Jones 1984), and algae commonly grow on the carapace of many species of turtles, including *C. longicollis* (Edgreen *et al.* 1953; Burgin and Renshaw 2008). We visually assessed algal coverage and classified individuals as having ≤ 1/3 coverage, or > 1/3 coverage.

We measured secondary available production as the standing-crop biomass of potential prey items, sampling wetlands once per month from December 2012 to February 2013. On each occasion, we conducted 4 time-constrained (30 s) searches in each pond by agitating the sediment and searching in the littoral zone around available structures (e.g., rocks, debris, macrophytes) with the use of a 34 cm x 28 cm dipnet (250 µm mesh). Samples were preserved in 90% ethanol for later sorting. In the lab, they were placed in a sorting tray divided into 16 sections and examined until 2 min of searching revealed no further items. Prey items were dried on absorbent paper for 10 min before weighing (+0.01

g) (Roe *et al.* 2011). We only considered potential prey items that are known to be eaten by *C. longicollis* (see Chessman *et al.* 1984; Georges *et al.* 1986).

Reproduction

Adult female turtles were transported to the University of Canberra for X-rays (AJEX Meditech Ltd; Model: AJEX160H; settings: 50 Kv, 1.20 mAs, 0.02 s, 70 cm high), and then released within seven days at their point of capture. Egg length (EL) and egg width (EW) were measured with callipers from the X-ray films, and egg volume (EV) was estimated with the formula

$$EV = \pi * X * Y^2/6$$

where X is the EL and Y is the EW (Vanzolini 1977).

Growth rates and movements

We considered two situations: a long-term evaluation (animals trapped in 2006-2007 and recaptured in 2011-2014, spanning a drought-wet period; Roe *et al.* 2011), and a short-term (animals captured and recaptured in 2011-2014, during a wet period only). We then compared growth rates among turtles from natural, rural and suburban areas considering the long term and the short term situation. Annual growth was measured as change in carapace length (CL), divided by the fraction of the approximately six-month growing season (15 September – 15 March) elapsed between captures. We only included individuals in the analysis if they were recaptured in the same study area and if the period between captures spanned at least one-half of a growing season. Individuals were assumed to have grown appreciably only if the growth increment exceeded the accuracy of measurements (± 0.5 mm); where the growth increment was < 0.5 mm, individuals were considered not to have grown appreciably and were excluded from the analysis of growth rate. The proportion of individuals that grew appreciably was also determined for each study site. The analysis of growth was done in accordance with the previous *C. longicollis* study during drought to allow comparisons (Roe et al 2011). For movement analysis, we assessed if recaptured individuals had moved among study sites, considering both long- and short-term recapture intervals. We calculated minimum straight-line distances animals moved with ArcGIS (version 9.3.1: ESRI 2009).

Demographic Parameters

We compared proportion of females, estimated population size, size frequency distributions, survivorship and recapture probability among our study sites. For estimation of population size, we used the Horvitz-Thompson type estimator (Seber 1982):

$$N = \frac{n}{p}$$

where *N* is the estimated population size, *n* is the number of unique turtle captures in each pond, *p* is the capture probability. Data for demography analysis was considered from November 2011 to March 2014, and done as in Roe *et al.* (2011) for comparisons.

Data analysis

Statistical analyses were performed with SPSS (Version 21), Program MARK version 7.1 (White and Burnham 1999), and and SAS Version 9.1 (SAS Institute 1999). The assumptions of normality and homogeneity of variances were checked by analysis of residuals and when data failed to meet these assumptions, data were transformed to approximate normal distributions and equal variances; otherwise non-parametric tests were used. Statistical significance was accepted at the $\alpha= 0.05$ level unless specified otherwise.

Road density was compared among study sites with a Kruskal-Wallis Test. We compared primary (TP and TN) and secondary (prey biomass) productivity among study sites using analysis of variance (ANOVA). TP and prey biomass were $\log_{10}$ transformed and TN was square root transformed to meet the assumptions normality. We compared our second measure of primary productivity (proportion of algal growth on turtles' carapaces) among study areas with a chi-square contingency analysis.

The proportion of mature females that were gravid was compared among sites with a chi-square contingency analysis. We used multiple linear regressions to examine whether turtle size metrics (CL, CW, and CL x CW interaction) were predictors of the egg metrics (clutch size, EL, EW, and EV). We used analysis of covariance (ANCOVA) to test whether clutch sizes differed among sites, with site as the independent variable, clutch size as the dependent variable, CL as the covariate, and the interaction of site and CL.

The proportion of individuals showing appreciable growth was compared among study areas with a series of chi-square contingency analyses (juveniles and adults separate). Growth rates were compared among sites using ANCOVA, with site as the independent variable, $\log_{10}$ carapace growth rate as the dependent variable, initial CL as the covariate, and the interaction of site and initial CL. Growth rates analysis were performed for both long-term and short-term recaptures.

Proportion of females was compared with ANOVA, with site as the independent variable, and proportion of females as the dependent variable. Turtle population size was compared with ANCOVA, with site as the independent variable, estimated population size as the dependent variable, and wetland surface area as the covariate. Overall differences in size-frequency distributions among sites were examined with a chi-square test using the PROC FREQ procedure in SAS. We followed the overall test with a series of chi-square tests to examine in which size classes differences occurred. We used the Dunn-Sidak correction to lower the significance ($\alpha < 0.004$) for these comparisons.

Survivorship and recapture probability were estimated with the use of Cormack-Jolly-Seber (CJS) open population capture-recapture models in Program MARK. We estimated parameters among groups (adult male, adult female, and juvenile), sites (nature reserve, rural, and suburb), and over time (sampling occasions). We collapsed capture histories into two approximately even occasions per year owing to the different sampling effort in our fixed and occasional trapping sites. We started with models where survivorship (Φ) and capture probability (ρ) were allowed to vary over time, among groups and among sites. We then fitted a series of reduced parameters models and ranked them based on Akaike's Informaiton Criterion (AIC). If competing models had AIC values ≤ 2.0, we considered them as having some support (Lebreton *et al.* 1992). We assessed the fully saturated model's adequacy to describe the data using a bootstrap goodness-of-fit test with 500 simulations and an overdispersion parameter ($\hat{c}$) was derived by dividing the model deviance by the mean of the simulated deviances (Cooch and White 2014). If there was evidence for overdispersion ($\hat{c} > 1$), we adjusted the models with the derived $\hat{c}$ to improve model fit and calculated a quasi-likelihood estimator, QAIC_c (Burnham and Anderson 1998). All parameters were estimated using model averaging.

Results

Anthropogenic impact

There was a difference in road density among study sites ($X^2 = 10.59$, df = 2, $P = 0.005$), with the suburban site having higher values (mean, SE, Range) (17.88 ± 0.83 km/km^2

[15.67-19.29]), followed by rural (1.86 ± 1.17 km/km^2 [0.0-5.76]), and nature reserve (0 km/km^2).

Primary and secondary productivity

The nature reserve and rural ponds had similar TP and TN, and higher than suburban ponds (TP: ANOVA: $F_{2,39} = 10.08$, $P < 0.001$; TN: ANOVA: $F_{2,39} = 47.90$, $P < 0.001$; Table 4.1). Carapace algal coverage was similar between suburban and rural turtles ($X^2 =$ 3.36, df = 1, $P = 0.07$), and both were higher than nature reserve turtles ($X^2 = 40.1$, df = 2, $P < 0.001$; Table 4.1). In addition, there was no difference in prey biomass among sites (ANOVA: $F_{2,39} = 0.35$, $P = 0.70$; Table 4.1).

Reproduction

Of 299 adult females, only 8.4% were gravid. The percentage of gravid females did not vary among sites (nature reserve: 10.7%; rural 5.8%; suburb: 8.4%) ($X^2 = 0.70$, df = 2, $P =$ 0.71). Turtles had shelled eggs only from October through December in each year (Fig. 4.2). After controlling for carapace length, clutch sizes were similar among study sites (ANCOVA site: $F_{2,19} = 0.72$, $P = 0.50$; CL: $F_{1,19} = 24.57$, $P < 0.005$; Table 4.2). The interaction between site and CL was not significant ($P = 0.60$) and was dropped from the analysis to increase power. Egg length ($F_{3,18} = 0.32$, $r^2 = 0.05$ $p = 0.81$) and egg volume ($F_{3,18} = 1.96$, $r^2 = 0.25$ $p = 0.16$) were not correlated with turtle size metrics, but egg

Table 4.1. Primary and secondary productivity measurements in ponds inhabited by *Chelodina longicollis* among study sites, Australian Capital Territory, Australia (Mean, SE, Range).

	Primary			Secondary
	TP (mg/l)	TN (mg/l)	Carapace algal cover*	Prey biomass (g)
Nature Reserve	0.11 ± 0.01^{A}	1.42 ± 0.09^{A}	$0\%^{A}$	2.66 ± 0.39^{A}
(n = 15)	(0.04-0.26)	(0.89.1-2.28)		(0.96-5.50)
Rural	0.08 ± 0.01^{A}	1.47 ± 0.08^{A}	$47\%^{B}$	3.35 ± 0.58^{A}
(n = 15)	(0.05-0.15)	(1.03-2.01)		(0.27-6.58)
Suburb	0.05 ± 0.01^{B}	0.61 ± 0.03^{B}	$62\%^{B}$	$2.52 \pm 0.56_{A}$
(n = 12)	(0.02-0.09)	(0.46-0.76)		(0.52-6.89)

* Percentage of individuals showing mid- to high algal growth on the carapace (> 1/3 coverage). Superscript letters demonstrate differences among groups.

width was positively correlated with body size ($F_{3, 18}$ = 3.51, r^2 = 0.37 p = 0.04; Predictor variables: CL: Beta = 7.11, p = 0.03; CW: Beta = 8.32, p = 0.02; CL x CW interaction: Beta = - 14.59, p = 0.02).

Growth and movements

After controlling for carapace length, there was a difference in turtle growth rates among sites during the long-term interval (ANCOVA site: $F_{2,39}$ = 12.49, $P < 0.005$; CL: $F_{1,39}$ = 95.21, $P < 0.005$), with suburban turtles growing fastest, followed by rural, and then nature reserve turtles (Table 4.3, Fig. 4.3). The interaction between site and CL was not significant (P = 0.52) and was removed the analysis to increase power. There was no difference in growth rates among study sites during the short-term interval (ANCOVA site: $F_{2,51}$ = 2.22, P = 0.12; CL: $F_{1,51}$ = 32.49, $P < 0.005$; Table 4.3, Fig. 4.3). The interaction between site and CL (P = 0.55) was also removed from the analysis. The percentage of juveniles and adults growing appreciably did not differ among study sites during the long-term (juveniles: X^2 = 1.73, df = 2, P = 0.42; adults: X^2 = 3.37, df = 2, P = 0.18) or short-term intervals (juveniles: not computed as growth was a constant; adults: X^2 = 3.80, df = 2, P = 0.14; Table 4.3).

We recaptured 32 turtles that were originally encountered in the nature reserve in 2006 – 2007, of which eight were recaptured in suburban ponds during 2011 – 2014, displacing distances of (mean, SD, Range) 1446.2 ± 1220 m (540 – 3800 m). We also recaptured 28 individuals originally encountered in the suburban ponds in 2006 – 2007, three of which were recaptured in the nature reserve and four in the rural site during 2011 – 2014, moving distances of 3118.8 ± 1540 m (1575 – 6020 m). All of the 17

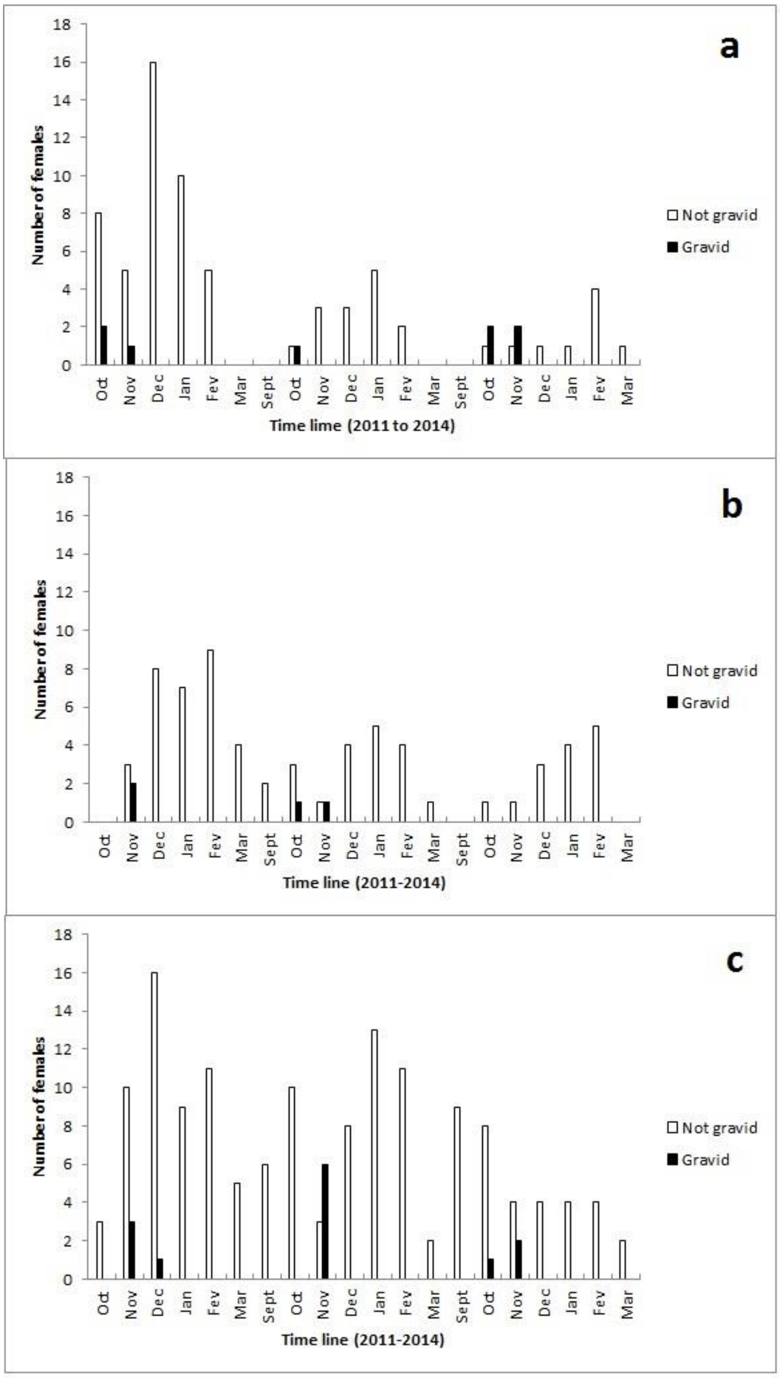

Figure 4.2. Gravid females *Chelodina longicollis* inspected through X-ray in nature reserve (a), rural (b), and suburban (c) sites, in Australian Capital Territory, Australia. X-rays performed from October 2011 to March 2012, September 2012 to March 2013, September 2013 to March 2014.

Table 4.2. Clutch size and egg measurements of gravid female *Chelodina longicollis* (through X-ray evaluation) from different study sites, Australian Capital Territory, Australia (Mean, SE, Range; CS: clutch size, EL: egg length, EW: egg width, EV: egg volume)

	CS (n)	EL (mm)	EW (mm)	EV (mm^3)
Nature Reserve	10.8 ± 0.8	29.9 ± 0.7	21.1 ± 0.3	7009 ± 312
(n = 7)	(8.0-14.0)	(28.1-31.7)	(20.1-22.5)	(6151-8319)
Rural	14.2 ± 0.9	29.7 ± 1.4	21.1 ± 0.3	6942 ± 501
(n = 4)	(13.0-17.0)	(27.5-34.0)	(20.1-21.5)	(5822-8254)
Suburb	12.5 ± 0.8	29.7 ± 0.4	20.7 ± 0.3	6713 ± 207
(n = 12)	(8.0-17.0)	(27.4-32.6)	(19.1-22.7)	(5762-8088)

Table 4.3. Growth rates of eastern long-necked turtles (*Chelodina longicollis*), after controlling for carapace length (ANCOVA), and recaptures for juveniles (J) and adults (A), spanning long-term (drought-wet) and short-term (wet) conditions, Australian Capital Territory, Australia.

		Recaptures (*n*)		Percentage growing		Carapace growth rate (mm/yr)[a,b]	
Period	Group	J	A	J	A	*N*	Mean ± SE (range)
Long-term	Nature Reserve	5	19	100	47	14	4.4^{A} ± 1.0 (0.79-12.44)
2006-2014	Rural	5	11	80	73	12	3.8^{B} ± 0.8 (0.50-9.14)
	Suburb	3	19	100	74	17	4.5^{C} ± 0.8 (0.93-13.88)
Short-term	Nature Reserve	4	25	100	48	16	5.7^{A} ± 1.7 (0.94-27.31)
2011-2014	Rural	8	3	100	67	10	8.0^{A} ± 3.0 (0.83-26.83)
	Suburb	11	24	100	75	29	7.7^{A} ± 1.4 (0.63-28.01)

[a] Based on a growth year spanning the typical activity season (15 Sep to 15 Mar).

[b] Statistical analysis were performed with $\log_{10}$ growth rate values to meet the assumption of normality.

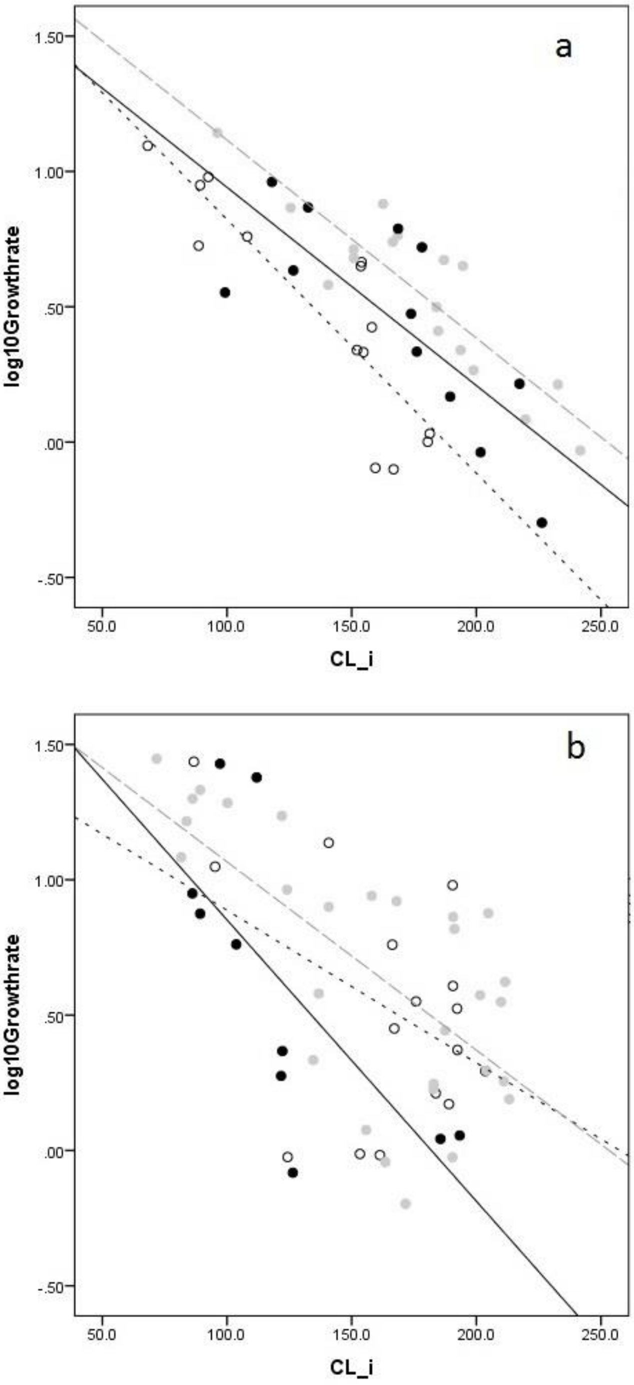

Figure 4.3. Relationships of growth and initial carapace length (mm) in *Chelodina longicollis* inhabiting nature reserve (open circles, smaller black dashed line), rural (black filled circles, solid line) and suburban (grey filled circles, larger grey dashed line) habitats, during 2006-2014 period (a) and 2011-2014 (b) period, Australian Capital Territory, Australia.

recaptures originally encountered in the rural sites in 2006 – 2007 were recaptured in rural sites during the 2011 – 2014 sampling. Considering the short-term interval, none of the turtles recaptured in the present study from any of the three sites were trapped in different study areas during the 2011 – 2014 period.

Demographic Parameters

We made 782 captures of 655 different turtles. There was no difference in proportion females (Mean, SE, Range) among our sites (Nature Reserve: 0.49 ± 0.18 [0.28-0.72]; Rural: 0.38 ± 0.14 [0.21-0.54]; Suburb: 0.45 ± 0.12 [0.29-0.57]) (ANOVA: $F_{2,10} = 0.35$, $P = 0.60$). Population sizes increased from nature reserve to rural to suburban study areas, but after controlling for wetland surface area, population sizes did not differ among sites (Nature Reserve: 47.6 ± 17.5 individuals [14.0-110.6]; Rural: 110.2 ± 36.6 ind. [10.2-224.3]; Suburb: 156.3 ± 35.3 ind. [74.2-231.0]; ANCOVA: site: $F_{2,10} = 2.19$, $P = 0.16$; wetland surface area: $F_{1,10} = 1.71$, $P = 0.22$). The interaction between site and wetland surface area was not significant ($P = 0.09$) and was removed from the analysis to increase power. Size-frequency distributions differed among sites (overall $X^2 = 87.2$, df = 24, $p < 0.001$), with significant differences within 60.1 – 75mm PL ($X^2 = 12.0$, df = 2, $p < 0.004$) and 105.1 – 120mm PL size classes ($X^2 = 14.1$, df = 2, $p < 0.004$), with more individuals in the rural site in both cases, as well as in the 165.1 – 180mm PL size class, with more individuals in the rural and suburban sites than the nature reserve ($X^2 = 15.0$, df = 2, $p < 0.004$; Fig. 4.4). In the capture-mark-recapture analysis, the model with most support had survivorship constant over time and among groups and sites, and capture probability varying according to site, with rural turtles with the lowest values (Table 4.4, 4.5). The other competing models had no support according to Δ QAIC$_c$ values (Table 4.4).

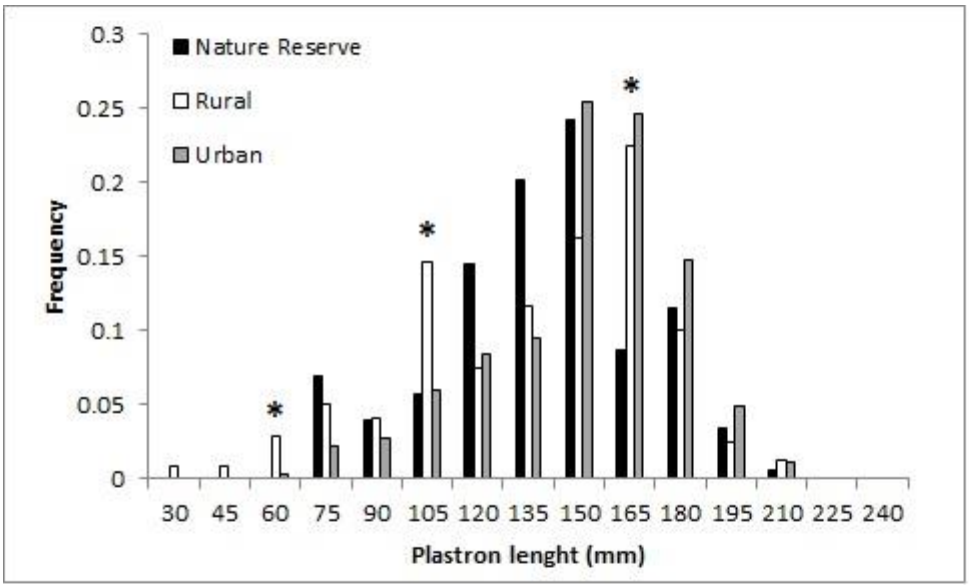

Figure 4.4. Size-frequency distributions of *Chelodina longicollis* among study sites, Australian Capital Territory, Australia. Asterisk indicated statistical difference.

Table 4.4. Models of survivorship (Φ) and capture probability (ρ) of *Chelodina longicollis* over time, among sites (nature reserve, rural, and suburb), and among groups (adult male, adult female, and juvenile) in the Australian Capital Territory, Australia, 2011-2014. Models were compared and ranked with a quasi-likelihood Akaike's Information Criterion ($QAIC_c$) estimator corrected for overdispersion ($\hat{c}$ = 1.51).

Model	$QAIC_c$	Δ $QAIC_c$	Weight	Parameters	Deviance
Φ (.) ρ (site)	491.7	0.00	0.52	4	115.8
Φ (site) ρ (.)	493.8	2.03	0.19	4	117.8
Φ (.) ρ (.)	494.7	2.97	0.12	2	122.8
Φ (group) ρ (.)	495.6	3.81	0.08	4	119.6
Φ (.) ρ (group)	496.4	4.62	0.05	4	120.4
Φ (site x group) ρ (.)	498.1	6.37	0.02	10	109.9
Φ (.) ρ (site x group)	498.6	6.88	0.02	10	110.4
Φ (site x group) ρ (site x group)	508.0	16.26	0.00	18	103.1
Φ (.) ρ (site x group x time)	552.6	60.89	0.00	46	85.9
Φ (site x group x time) ρ (.)	554.1	62.40	0.00	46	87.5
Φ (site x group x time) ρ (site x group x time)	641.8	150.06	0.00	90	66.5

Table 4.5. Estimates of survivorship (Φ) and capture probability (ρ) for *Chelodina longicollis* among different sites and groups in the Australian Capital Territory, Australia, 2011-2014. Parameters were derived as weighted averages based on their quasi-likelihood Akaike's Information Criterion ($QAIC_c$) values, adjusted for model overdispersion. Results expressed in Mean ± SE.

Site	Group	Φ (bi-annual)	Φ (annual)	ρ * (bi-annual)
Nature Reserve	Male	0.688 ± 0.076	0.473 ± 0.005	0.117 ± 0.028
	Female	0.702 ± 0.074	0.492 ± 0.005	0.121 ± 0.029
	Juvenile	0.687 ± 0.076	0.471 ± 0.005	0.118 ± 0.029
Rural	Male	0.648 ± 0.078	0.419 ± 0.006	0.077 ± 0.022
	Female	0.652 ± 0.077	0.425 ± 0.005	0.079 ± 0.022
	Juvenile	0.639 ± 0.079	0.408 ± 0.006	0.077 ± 0.022
Suburb	Male	0.671 ± 0.078	0.450 ± 0.006	0.099 ± 0.029
	Female	0.686 ± 0.076	0.470 ± 0.005	0.102 ± 0.029
	Juvenile	0.668 ± 0.079	0.446 ± 0.006	0.101 ± 0.029

*Capture probabilities showed differences among sites according to model selection.

Analyses using only the fixed trapping sites supported the same highest ranked model as analyses using both fixed and occasional sampling sites.

Discussion

Long-term studies of turtles inhabiting urban landscapes have focused specifically on demographic parameters and vital rates before and after major habitat alterations (e.g., Plummer and Mills 2008; Plummer *et al.* 2008; Eskew *et al.* 2010). While we were not able to examine turtle populations prior to urban development, our study is unique in that we evaluated not only changes in degree of urban development over time and space, but also other potentially interacting stressors such as climate and invasive predators. Relative to the initial 2006 – 2007 sampling when the system was in drought (mean 464 mm/yr, El Niño period, van Dijk *et al.* 2013) and at the early stages of urban development (Rees *et al.* 2009; Roe *et al.* 2011), our recent sampling from 2011 – 2014 coincided with higher rainfall (mean 602 mm/yr, La Niña event, Beard *et al.* 2011) and a marked increase in urbanization. In addition, a fence was recently built to exclude non-native animals and isolate the nature reserve from encroaching suburban hazards (Ferronato *et al.* 2014). Such a longitudinal study across a gradient of anthropogenic impact and following such changes allowed us to examine spatial and temporal responses in behavior, demography, and vital rates, yielding insight into the mechanisms related to turtle persistence in suburban systems.

The evidence of increased urbanization in the system (Gungahlin suburbs) over the last five years includes a 79% growth in human population (Australian Bureau of Statistics 2013), a 76% increase in traffic volume (Territory and Municipal Services, R. Shoukrallah, personal communication), and a 2.3 times higher road density in our study compared to previous measurement of this parameter (Roe *et al.* 2011). Such an increase in urbanization, especially regarding road density and traffic volume, could pose a threat for turtles with marked propensity for overland movements, although our measures of various behavioral, demographic, and population vital rates together with those of earlier studies suggest otherwise (Roe *et al.* 2011). The apparent resilience of *C. longicollis* to such threats is in contrast with demographic responses of several other species to heavy road density and traffic volume elsewhere (Gibbs and Shriver 2002; Marchand and Litvaitis 2004; Aresco 2005; Nafus *et al.* 2013).

Although we considered habitats in the context of being more or less influenced by anthropogenic stressors, we were also interested in understanding potential differences in productivity. Urban areas may have higher productivity and nutrient loads owing to human subsidized resources (DeStefano and DeGraaf 2003; Shochat *et al.* 2006), which can ultimately influence growth rates and reproductive output in turtles (Gibbons 1967; Brown *et al.* 1994; Lindeman 1996). The contrasting results from the two measures of primary productivity in this study could have been influenced by differences in the uptake of resources by organisms and variation in the availability of nutrients during sampling (Jones 1984; Müller 2000), though no clear differences existed among sites. However, availability of food resources for turtles was similar among study sites, suggesting that productivity did not differ in ways relevant to turtle population regulation, a finding in agreement with previous estimates of food availability during drought (Roe *et al.* 2011). The lack of elevated productivity may be related to the lack of sewage contamination in our system, which can be a significant source of nutrient input in urban areas elsewhere (Galbraith *et al.* 1988; Souza and Abe 2000; Marques *et al.* 2008).

Our growth rate results demonstrate how access to resources and foraging opportunities are likely the primary factors influencing turtle growth in our system. During drought, turtles in suburban areas grew five times faster than those in the nature reserve in the same system (Roe *et al.* 2011), even though they had similar prey biomass in the ponds. The authors hypothesized that the constant availability of water extended the activity period (and thus foraging opportunities) for turtles in suburbs, while ponds in the nature reserve dried and most turtles aestivated on land. Our results support this hypothesis, as growth rates over long-term periods spanning both dry and wet periods were higher for suburban turtles compared to other environments, while growing at similar rates during wet times. During the wet period (2011-2104), all ponds remained flooded across environments and no turtles were observed to estivate on land despite extensive searches and radiotelemetry (Ferronato, unpubl. data). Growth rates of animals, including *C. longicollis*, are strongly influenced by rainfall patterns in wet-dry cycles characteristic of much of Australia (Kennett and Georges 1990; Madsen and Shine 2000; Madsen *et al.* 2006; Greenville *et al.* 2013; Wardle *et al.* 2013).

Turtles in urban systems may have higher fecundity than in natural settings (Gibbons and Tinkle 1969; Brown *et al.* 1994; Lindeman 1996), but we did not detect variation among sites in any measure of reproductive biology, including reproductive season, clutch sizes, and percentage of gravid females. That our measures of fecundity were similar across environments is again likely related to similar food availability among sites. *Chelodina longicollis* can lay up to three clutches in a reproductive season in the Murray River and in Gippsland, Victoria (Parmenter 1985; Kennett *et al.* 2009), but we found no evidence of multiple clutches based on X-ray analysis of females recaptured within a breeding season, a finding corroborated by a previous study in the Canberra region (Vestjens 1969) and likely reflecting climactic constraints on the length of reproductive season, from October until December. Even though we do not have information on reproductive output of *C. longicollis* during drought in our system, females estivate on land for several months in response to wetland drying (Rees *et al.* 2009), in addition to cessation of reproduction during unfavourable conditions at other locations in south-eastern Australia (Kennett and Georges 1990).

The observation of similar population sizes among study sites at first suggests a different dynamic from the previous drought, where suburban turtles were nearly three times more abundant than nature reserve turtles (Roe *et al.* 2011). However, despite statistical analysis, abundance in nature reserve ponds was still 3.2 and 2.3 times lower than the suburb and rural site, respectively, a difference that could be biologically meaningful but biased by low sample size. For instance, even though the same ponds were sampled in each study, sample sizes in the current study were smaller owing to the construction of the fence that required the natural site to be divided into two independent samples, reducing power in the analysis. While nature reserve turtles resumed growth and reproduction during the recent wet conditions, perhaps not enough time has passed for a population-level response to be realized. Additionally, at the same time that the drought broke, the predator-proof fence was erected, isolating that population and preventing remigrations of individuals that had left for the suburban ponds during drought. Indeed, many more turtles were encountered on the outside of the fence following the return of rainfall, which likely represent individuals attempting to return to the flooded ponds in the nature reserve (Ferronato *et al.* 2014). Thus, immigration into nature reserve ponds was eliminated, causing both high mortality and forcing them into other ponds.

The observation of animals in the smaller size classes in all study sites indicates that recruitment has continued despite expanded urbanization. One of the typical challenges facing turtles in urban landscapes is limited recruitment owing to high predation rates and lack of nesting habitats (Spinks *et al.* 2003; Marchand and Litvaitis 2004). The presence of recruitment across all levels of anthropogenic impact examined here is a signal that some females are still safely reaching nesting areas, eggs are successfully incubated, and some hatchlings are capable of traveling to water. Although survivorship did not vary across study sites based on capture-mark-recapture estimates, a concurrent radio-telemetry study demonstrated that adult female suburban turtles had lower annual survivorship (0.67) compared to females from the nature reserve (1.00, Ferronato, unpubl. data), where most mortality was on roads. However, the radio-telemetry study focused only on females, and we identified localized hotspots that could have biased mortality differences in the telemetry owing to small sample sizes (Ferronato, unpubl. data). The overall mortality in the broader study area could be diffuse at the meta-population scale, yet still significant on local scales. Regardless, survivorship estimates in the present investigation are especially low for *C. longicollis* (Roe *et al.* 2009) and compared to other freshwater turtles (Shine and Iverson 1995), so we question the accuracy of these survival rates. Considering the biology of *C. longicollis* and its ability for frequent and long-distance inter-wetland movements (Ryan and Burgin 2007; Roe and Georges 2008b; Roe *et al.* 2009), there is potential for high emigration to ponds outside the sample locations, which would be interpreted as “mortalities” in our CJS models (Cooch and White 2014). We did not consider using Robust Design approach to account for emigration, as females were temporarily removed from the populations for X-ray analysis, which would have violated the assumptions of such models.

Previous research has demonstrated the high vagility of *C. longicollis*, suggesting that single wetlands should not represent the minimum habitat unit harbouring a population (Roe and Georges 2008b; Roe *et al.* 2009). Rare dispersal events of up to 5.2

km have been described in dunes lakes in an undisturbed setting in south-eastern Australia (Roe *et al.* 2009). Based on long-term recaptures, the present data indicate that such long distance movements (up to ~ 6 km) also occur within natural-urban gradients, suggesting that the turtles behave similarly with regards to inter-wetland movements for dispersal or migration in suburban landscapes where roads must be crossed. Such movements are important for maintaining connectivity and gene flow among populations (Hansson 1991; Coulon *et al.* 2004), a factor that should be taken into consideration when managing risks for mobile aquatic species living in urbanized landscapes (Pickett *et al.* 2001; Garden *et al.* 2006). It also underscores the importance of these movements for rescuing from stochastic events such as drought. However the current design of the pest-fencing is disrupting this dynamic in response to wet-dry cycles (Rees *et al.* 2009; Roe *et al.* 2011; Ferronato *et al.* 2014), and causing high mortality for turtles attempting to pass (Ferronato *et al.* 2014). On the other hand, these long distance movements demonstrate that our sites do not satisfy the assumption of independence. However, such important behavior would have not been documented in short-term studies or if we had only sampled wetlands distant from each other (e.g. 10 km apart). Moreover, another limitation in our design is that the construction of the fence enclosure in the nature reserve isolated that population from exchange with other nearby ponds.

Conclusions

Together, our findings of similar vital rates, demography, and the presence of recruitment in all study sites indicate that *C. longicollis* is resilient to urbanization in our system. Perhaps *C. longicollis'* ability to move overland and settle in different habitats (Kennett and Georges 1990; Roe and Georges 2008a,b; Roe *et al.* 2009), in addition to its opportunistic carnivore feeding behavior (Chessman *et al.* 1984; Georges *et al.* 1986) is part of its successful colonization and persistence in suburban ponds. Additional evidence for *C. longicollis* resilience is its record of establishment across a range of urban settings over broad spatial scales (Ryan and Burgin 2007; Rees *et al.* 2009; Roe *et al.* 2011; Stokeld *et al.* 2014). Other generalist species of freshwater turtles have also persisted and even thrived in wetlands under some degree of anthropogenic influence elsewhere (Lindeman 1996; Souza and Abe 2000; Plummer *et al.* 2008; Ryan *et al.* 2008; Lathouder *et al.* 2009; Price *et al.* 2013; Germano 2010).

By examining population dynamics in the same system over time (Rees *et al.* 2009; Roe *et al.* 2011) we documented the strong influence of climate (e.g. rainfall) on population dynamics, supporting the idea that resources in natural habitats oscillate more while suburban environments are more stable, buffering turtles from such fluctuations in environmental conditions (Rees *et al.* 2009; Roe *et al.* 2011). As a consequence of these marked differences in habitat conditions between natural and suburban systems, we detected differences in growth and behavior of nature reserve turtles between dry and wet period, while suburban turtles showed relatively similar ecology and behavior despite the weather conditions. We could also demonstrate the interactive way on which urbanization, climate and invasive predators influenced the ecology and demography of *C. longicollis*, highlighting the importance of considering and managing contiguous and broad patches of habitat that link suburban systems with surrounding landscapes as a whole rather than as isolated units, as turtles can disperse long distances across these gradients influencing population or metapopulation dynamics. Future research should focus on the monitoring of the nature reserve population enclosed by the predator-proof fence in order to understand pros and cons of this conservation tool, and evaluate effectiveness of possible mitigation actions such as water under-passages, which allow turtle movements but impede foxes

(Long & Robley, 2004). Despite our increased understanding of *C. longicollis* population dynamics, our study lacks replication as we only studied turtle populations under one gradient of urbanization and also only one population under the effects of pest-fencing. Additionally, even though our longitudinal study compared population dynamics after five years, the study duration is still relatively short compared to the turtle life-spans (Gibbons 1987; Congdon *et al.* 2003), making further monitoring essential for our full understanding of turtle dynamics in suburban landscapes over extended time periods.

Chapter 5

First record of hatchling overwintering in a Chelid turtle

The manuscript will be submitted for publication in the journal **Copeia** as: Ferronato, B.O., Roe, J.H., Georges, A. First record of hatchling overwintering in a Chelid turtle. Presented as submitted with minor formatting changes.

Abstract

Hatchling overwintering inside the natal nest is a strategy used by several Northern Hemisphere species of freshwater turtles. In the present study, we recorded for the first time hatchling overwintering in the nest by *Chelodina longicollis* (Chelidae) in southeastern Australia, during three reproductive seasons. Hatchlings spent on average 320 days inside the nest from the date eggs were laid until emergence. Some nests were carefully opened adjacent to the nest plug, one during winter and one in spring to confirm that eggs had hatched prior to winter. Despite our small sample size, we observed an intra-population dichotomous overwintering strategy, with hatchlings from one nest emerging in autumn and spending their first winter in the aquatic environment, and hatchlings from three nests overwintering in the nest and emerging in spring. These findings expand the phylogeny of turtles exhibiting hatchling overwintering behavior. Future research should evaluate whether this strategy is widespread among other long-necked turtles in temperate regions and examine physiological mechanisms involved in coping with winter temperatures.

Introduction

Time of emergence from the nest has profound ecological and evolutionary implications for egg laying species, including freshwater turtles (Gibbons and Nelson 1978; Costanzo *et al.* 2008; Gibbons 2013). Delayed emergence has been hypothesized as one of the strategies used by turtles to better coincide emergence with resource availability (Gibbons and Nelson 1978; Mitchell 1998; Costanzo *et al.* 2008; Buhlmann *et al.* 2009). The delay can be of a few days to several months after hatching (Wilson *et al.* 1999; Gibbons 2013; Lovich *et al.* 2014; Riley *et al.* 2014). Hatchling overwintering in the nest, also known as terrestrial hibernation in shallow nests, is one type of delayed emergence in temperate areas (Gibbons 2013), where hatchlings spend winter inside the natal nest and emerge the following spring (Costanzo *et al.* 2008; Gibbons 2013). Another strategy used by some species is to emerge from the nest in the fall, but hatchlings overwinter on land in refuges prior to reaching the wetland in spring (Muldoon and Burke 2012; Paterson *et al.* 2012). Overwintering in the nest may have costs and benefits. Direct costs may include nest mortality from freezing, flooding, predation, dehydration, and energy depletion (Gibbons and Nelson 1978; Packard 1997; Costanzo *et al.* 2008), while benefits may include accelerated growth by timing emergence with an environment in which thermal and food resources are increasing rather than decreasing (Gibbons and Nelson 1978; Costanzo *et al.* 1995, 2008). Hatchling overwintering in the nest has been mainly observed in turtle species in the Northern Hemisphere, especially in the family Emydidae (reviewed by Gibbons 2013), with only one record of an Emydidae turtle living in the Southern Hemisphere (Bager *et al.* 2007).

Long-necked turtles are members of the family Chelidae, which occur in Australia, South America, New Guinea and the Indonesian Island of Roti (Georges and Adams 1992;

Seddon *et al.* 1997). *Chelodina longicollis* is a common long-necked turtle with a broad geographic distribution in south-eastern Australia, occurring in several freshwater habitats (reviewed by Kennett *et al.* 2009). *C. longicollis* is known to mate in early spring (September), lay eggs in late spring and early summer (October - January), and emerge from nests in autumn (April – May; Vestjens 1969; Parmenter 1985). Despite the fact that delayed emergence had been documented for some turtle species in Australia (Goode and Russell 1968; Kennett *et al.* 1993 a,b; Doody *et al.* 2001), hatchling overwintering inside the nest has not yet been documented, although several authors have suggested nest overwintering by *C. longicollis* in the wild (Chessman 1978; Kennerson 1980; Dalem and Burgin 1996). In the present study, we document for the first time hatchling overwintering inside the natal nest by *C. longicollis*, documenting the entire incubation period and nest emergence, and suggest future studies that would help to elucidate this behavior and mechanisms involved in Chelid turtles.

Methods

We searched for and monitored *C. longicollis* nests in Gungahlin region, Australian Capital Territory (ACT), south-eastern Australia, from November 2011 to October 2014. The ACT climate is temperate, with mean monthly maximum air temperature ranging from 11°C in July to a peak 27°C in January and February, and a mean monthly minimum air temperature ranging from 0°C to 13°C in the same months, in addition to a mean annual rainfall of 600 mm (Palmer-Allen *et al.* 1991). Nests were located around ponds in three locations, including the Ginninderra Experiment Station (Commonwealth Scientific and Industrial Research Organization – CSIRO), which consists of areas with native grasses and eucalypts, in addition to areas with crops and pastures (Webster and Butler 1976), the Gungahlin suburbs, an industrial and residential area with high road densities and managed suburban green spaces such as golf courses, suburban parks, gardens and sport ovals (see Rees *et al.* 2009; Roe *et al.* 2011), and in Mulligans Flat Nature Reserve, a 791 ha reserve composed of woodlands, grasslands, several ponds and the upper tributaries of Ginninderra Creek (Rees *et al.* 2009; Roe *et al.* 2011).

Nests were located by walking along the ponds during late spring and early summer (November-December), which corresponds to the nesting season in the region (Vestjens 1969). Once a nest was found, usually by visually locating the nest plug, we measured the distance from the water and carefully removed the nest plug, accessing the nest and taking measurements of the nest cavity and eggs. We then returned eggs to the nests, inserting an i-button that recorded temperature every two hours in the core of the nest. The nest plug was replaced and covered with chicken wire mesh to protect from fox predation and to capture emerging hatchlings to allow us to record dates of hatchling emergence. Nests were visually monitored during the incubation period, and monitored every other day during the expected time of emergence in autumn (March-April) (Vestjens 1969). We chose two nests that did not emerge by autumn and carefully opened adjacent to the nest plug, one during winter and other at the beginning of spring, to confirm whether eggs hatched prior to winter. Then, they were monitored again in the following spring every other day (September-November). Whenever there were signs of nest emergence, the mesh cover was removed and the nest accessed. We then recorded hatchling success and took measurements such as carapace and plastron length (mm), and body mass (g).

Results

We monitored 10 natural nests from 2011 to 2014, and in five of them we observed nest emergence. In four of those nests, hatchlings overwintered inside the nest and emerged in spring, and in another hatchlings did not overwinter and emerged in autumn (Table 5.1). In the other five nests there were no signs of nest emergence after 16 months. They were opened and all contained some unhatched eggs or hatchlings that had pipped but were dead within the shell (Table 5.1). Hatchling overwintering inside the nest was observed in each of the three years, and nest emergence occurred after (Mean, SD, Min., Max.) 320.2 ± 30.8 days (284–356 days), with hatching success ranging from 36 to 100% (Table 5.1). Incubation period of the nest that did not overwinter was 125 days, with a 92% hatching success (Table 5.1). Nests were placed by females at 25.6 ± 24.9 m (2–70 m) away from the ponds, nest depth and nest mouth width were 8.9 ± 1.4 cm (6.8–11 cm) and 5.9 ± 1.0 cm (4.5–7.5 cm), respectively. Egg length and width were 3.17 ± 0.10 cm (2.94–3.42 cm) and 1.99 ± 0.05 cm (1.84–2.19 cm), respectively, and hatchlings carapace length, plastron length and mass were 2.80 ± 0.12 cm (2.4–3.0 cm), 2.16 ± 0.07 cm (1.93–2.36 cm), and 4.28 ± 0.39 g (3.0–4.9 g), respectively.

Due to i-button failure or data overriding, we were able to record nest temperatures for the entire incubation period in only two nests in the 2013-2014 season, representing a clutch that did not overwinter and one that did from the same population (Table 5.1, Fig. 5.1). Temperatures inside of the nest that did not overwinter were 24.41 ± 4.28 °C (14.06–36.0 °C). For the overwintering nest, temperature for the first 125 days of incubation (up to the date of hatching for the non-overwintering nests) was 26.55 ± 6.11 °C (13.23–44.75 °C), and 11.94 ± 4.11 °C (3.74–23.93 °C) through the overwintering period until the time of emergence (Fig. 5.1). We were able to recover partial temperature data for two nests that successfully overwintered and emerged in spring, which recorded winter temperatures as low as 1.27 °C and 2.31 °C during the 2011-2012 season (Table 5.1).

Table 5.1. *Chelodina longicollis* nests monitored during three reproductive seasons in Gungahlin, Australian Capital Territory, Australia.

Season	Area	Found	Emergence	Overwintered	N. eggs	Hatching Success
2011-2012	Csiro_4	29/11/2011	19/11/2012	Yes	13	100%
	Csiro_5	29/11/2011	03/10/2012	Yes	11	82%
	Csiro_14	07/12/2011	-	-	14	0%
	Csiro_19	13/12/2011	-	-	12	0%
	Reserve_1	08/12/2011	-	-	9	0%
	Reserve_4	03/01/2012	-	-	10	0%
	Suburb_1	05/01/2012	-	-	11	0%
2012-2013	Suburb_8	07/12/2012	17/09/2013	Yes	10	100%
2013-2014	Csiro_21	26/11/2013	24/10/2014	Yes	11	36%
	Csiro_22	26/11/2013	31/03/2014	No	13	92%

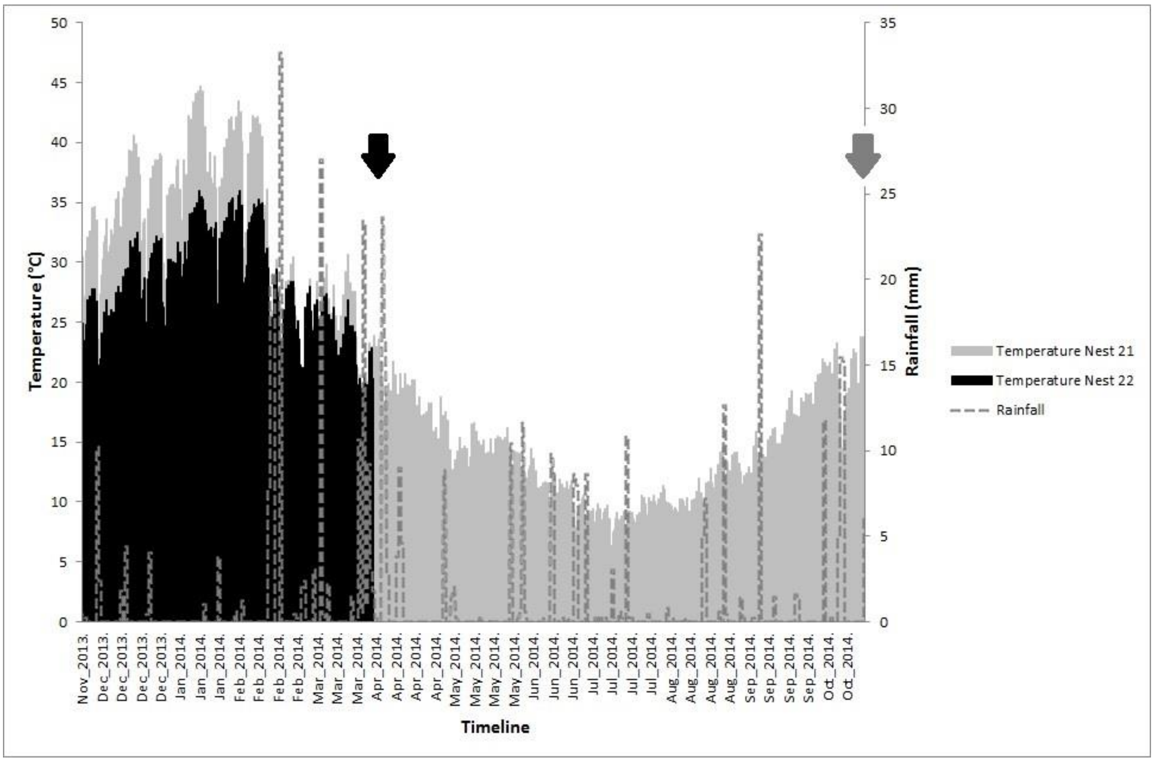

Figure 5.1. Incubation period and nest emergence of *Chelodina longicollis* from Gungahlin, Australian Capital Territory, Australia, during 2013-2014 nesting season. Nest 22 did not overwinter and hatchling emergence is depicted with black arrow. Nest 21 overwintered and hatchling emergence is depicted with grey arrow.

Discussion

To our knowledge, this is the first study to document hatchling overwintering inside the nest by a Chelid turtle. This is a significant finding for the long-necked turtles in the Southern Hemisphere, as such behavior has been mainly documented for Northern Hemisphere species.

The implications of this behavior relate to evolutionary aspects of nest emergence in long-necked turtles, in addition to the physiology and conservation of this species. Although previous studies have suspected delayed emergence by *C. longicollis* hatchlings owing to the records of hatchlings being captured in wetlands at the beginning of spring (Chessman 1978; Kennerson 1980; Dalem and Burgin 1996), this is the first study to confirm it. Even though delayed emergence from the nest has been reported in some Australian turtles (Carettochelyidae: *Carettochelys insculpta*; Chelidae: *Chelodina rugosa* and *Chelodina expansa*; Kennett *et al.* 1993a,b; Gibbons 2013), the behavior demonstrated here by *C. longicollis* is different from *C. insculpta*, *C. rugosa* and *C. expansa*. Pig-nosed turtles (*C. insculpta*) nest from mid-July to late October (dry season) and hatch from early October to early December (late dry to early wet season; Georges and Rose 1993), with an mean incubation period of 86 days (Doody *et al.* 2001). *C. insculpta* hatchlings go through embryonic aestivation and delay hatching (17 days on average) to time their emergence to match the onset of rainy season (Doody *et al.* 2001). *C. rugosa* lay eggs under shallow water of seasonally flooded wetlands during the wet and early dry season, when eggs remain in inundation-induced developmental diapause until floodwaters recede, development proceeds and hatchlings emerge with heavy rains or flooding in the following wet season (Kennett *et al.* 1993a,b). On the other hand, *C. expansa* incubation period lasts 324 days, with nests laid in autumn or early winter and eggs entering embryonic diapause throughout winter followed by hatching and emergence in late summer or autumn (Goode and Russell 1968; Booth 2002). *Chelodina longicollis* is unique in that there is apparently no embryonic diapause, as hatching occurs in autumn (Vestjens 1969; Parmenter 1985) followed by overwintering in the nest and emergence the following spring.

Current research indicates that hatchling overwintering inside the nest can be quite variable among and within populations (Costanzo *et al.* 2008; Gibbons 2013; Lovich *et al.* 2014; Riley *et al.* 2014), even including differences in timing of nest emergence among siblings sharing the same nest (see Costanzo *et al.* 2008). Research attempting to elucidate mechanisms and environmental cues responsible for intra-population variation in hatchling overwintering inside the natal nest are scarce (Riley *et al.* 2014). Some evidence suggests that environmental factors such as nest temperature, nest slope, percentage of bare ground surrounding nest, and risk of predation by Sarcophagid fly larvae may influence overwintering strategy in painted turtle hatchlings (Riley *et al.* 2014). Despite of our limited sample size, we have evidence that *C. longicollis* can exhibit a dichotomous hatchling overwintering strategy within the same population, though we have no conclusive information on possible triggers and environmental conditions that affect these variable responses. For example, temperatures inside overwintering nests tend to be cooler than non-overwintering nests (Riley *et al.* 2014), but we found an opposite result, with mean temperatures higher for the overwintering nest up to the time of emergence in the non-overwintering nest. We also observed hatchling overwintering in the nest in each year of the study (2011-2014), but interestingly such behavior was not reported in a previous investigation in the same region, where only fall emergence was documented (Vestjens 1969). Such findings suggest that hatchling overwintering in *C. longicollis* may vary among years, as reported for other species (Lovich *et al.* 2014). In addition, further research is needed to evaluate if the effect of drought-flood cycles in Australian environment could influence responses of hatchling overwintering in Chelid turtles, as there are evidences that rainfall and cool temperatures play a role in delayed emergence by hatchling turtles (Lovich *et al.* 2014).

The incubation period for *C. longicollis* that did not overwinter was in the range of other *C. longicollis* studies in Australia (Vestjens 1969; Parmenter 1985). The extended period of time inside the nest by *C. longicollis* hatchlings that overwintered (incubation plus overwintering = 320 days on average) is relatively similar to the length experienced by some species in the Northern Hemisphere (Gibbons and Nelson 1978; Costanzo *et al.* 1995; Wilson *et al.* 1999; Gibbons 2013), but temperatures experienced inside the nest during winter in our study site are much milder than those in USA and Canada (Packard 1997; Costanzo *et al.* 2000a; Riley *et al.* 2014). North American turtle hatchlings use physiological mechanisms, such as supercooling, to tolerate freezing temperatures (Costanzo *et al.* 2000b; Packard and Packard 2005), though further investigation would be necessary to investigate if *C. longicollis* perform such physiological mechanisms, though no nests experienced freezing temperatures in our study. *Chelodina longicollis* occurs up to altitudes of 800 m above sea level in New South Wales, where winter air temperature can be as low as - 13.9° C (Cooma Airport Weather Station, Australian Bureau of Meteorology; Dunsmore 1966).

Previous studies have detailed the importance of terrestrial habitats for numerous aspects of *C. longicollis*' behavior and population dynamics (Roe and Georges 2008 a,b; Rees *et al.* 2009). Hatchling overwintering is yet another critical aspect of ecology that occurs in terrestrial environments. Consequently, hatchlings may be vulnerable while in the nest to terrestrial disturbances outside of typical activity periods, such as changes in soil management practices, in addition to increased risk of predation by invasive predators, such as foxes (*Vulpes vulpes*; Thompson 1983; Spencer *et al.* 2006) and fire ants (*Solenopsis invicta*; Gibbons 2013).

Overwintering in the nest was once thought to be an unusual phenomenon observed in only a few North American turtle species, but after extensive research it is now believed to be a much more common behavior in many species worldwide (Gibbons 2013). The present findings of a Chelid species increases our knowledge in the phylogeny of turtles exhibiting hatchling overwintering behavior, and we suspect that this should also occur in other members of the Chelidae family inhabiting temperate regions of South America and Australia. Further studies are needed to investigate anecdotal accounts of overwintering in the range of *C. longicollis* elsewhere (Chessman 1978; Kennerson 1980; Dalem and Burgin 1996) to determine if this strategy is more widespread, as well as in other species of long-necked turtles, in addition to environmental cues, such as temperature, humidity or the effect of drought-flood cycles in such behavior.

Chapter 6

Synthesis

Considering my thesis goal of understanding the behavioral and population responses of *C. longicollis* to increasing urbanization and wetter climatic conditions, I was able to expand our current understanding of *C. longicollis* responses to numerous interacting challenges and opportunities. The present investigation gives new insights into the persistence and conservation of freshwater turtles in suburban landscapes and also opens new avenues for future studies, especially the responses of non-target species to emerging conservation practices such as the use of pest-fencing for conservation purposes. Specifically, I demonstrate the strong influence of rainfall on several ecological and behavioral parameters in *C. longicollis* inhabiting natural-urban gradients. It was also revealing to demonstrate how a fence can block movements, cause mortality and impede demographic responses in a turtle under the influence of wet-dry cycles (Ferronato *et al.* 2014). This study emphasises the importance of conducting long-term studies on turtles under the influence of anthropogenic stressors. I was able to show that *C. longicollis* is a resilient species with similar demography and vital rates among sites with different levels of human impact, and recruitment continued in all study sites following several changes in the system. In the following paragraphs I synthetize the main findings in each data chapter which address the specific objectives of this thesis.

Conservation fences have been used as a mitigation measure to reduce the impact of invasive predators on native wildlife (Long and Robley 2004; Bode and Wintle 2009; Hayward and Kerley 2009). Such fences can be effective and there are several examples of target species recovery within the enclosures (Hayward and Kerley 2009; Dickman 2012; Reardon *et al.* 2012). Nevertheless, there is a current debate as to whether such fences are the best option over the long-term owing to the associated costs and the small area being protected (Scofield *et al.* 2011; Innes *et al.* 2012; Woodroffe *et al.* 2014), in addition to some research demonstrating that fence can cause mortality in non-target species (Long and Robley 2004; Hayward and Kerley 2009; Bradby *et al.* 2014). This study is the first to investigate impacts of pest-fencing in a reptile community in Australia and demonstrate that impacts are species-specific, highlighting that *C. longicollis* can be highly impacted by the fence owing to direct and indirect mortality in the fence line and impeded dispersal and movements to rescue from stochastic events, such as drought (chapter two). Turtles were mainly trying to move from the suburbs' permanent ponds into the ephemeral ponds in the nature reserve when they met the fence and had their trajectory blocked. The identification of hotspots and hot moments of turtle encounters along the predator-proof fence can guide managers to implement mitigation measures at locations and times of highest concern.

When compared to previous research in our system (Rees *et al.* 2009; Roe *et al.* 2011), I was able to show that suburban and nature reserve turtles responded differently in wet conditions compared to drought conditions (chapter three). During drought, nature reserve ponds dried and turtles aestivated for extended periods on land or tried to move to permanent waters in the suburbs, while suburban turtles remained active as water levels were maintained in suburban ponds, making terrestrial aestivation unnecessary (Rees *et al.* 2009). I demonstrate how times of persistently high rainfall change the dynamic between nature reserve and suburban turtle populations. While the behavior of suburban turtles remained essentially unchanged, the return of rainfall and associated flooding liberated nature reserve turtles from dormancy, as they again became vagile and did not aestivate for extended periods on land. The few accounts of short-term aestivation on land were due to the fence blocking their movement. However, in addition to the changing behavioral dynamic, wetter times coupled with increased road density and traffic also brought upon higher mortality from vehicles in the suburban population, at least on localized scales. The findings of reduced survivorship of suburban turtles compared to nature reserve counterparts and the identification of hotspots of turtle's mortality on roads are valuable for conservationists and managers to implement mitigation on local scales.

Considering the capture-mark-recapture study, the present findings are in agreement with the hypothesis proposed by Rees *et al.* (2009) and Roe *et al.* (2011) in our system, as they suggested that the most important drivers for population regulation for *C. longicollis* are water availability and movement between permanent and ephemeral waters, in suburban and natural systems alike. I provide evidence in support of this hypothesis by demonstrating that turtles grew similarly among sites during the wet period, with similar breeding seasons and fecundity (chapter four). Moreover, I demonstrated the large number of turtles trying to migrate back to the ephemeral ponds in the nature reserve after re-flooding, only to have their movement blocked by the impenetrable fence (Ferronato *et al.* 2014). Most surprisingly was the long-term recapture of individuals moving long distances (up to 6 km) across sites despite the presence of several roads, underscoring the importance of such movements in suburban areas for connectivity, gene flow and population regulation among widely dispersed waterbodies (Hansson 1991; Coulon *et al.* 2004).

Looking at a more basic biological finding, I was able to demonstrate that *C. longicollis* hatchlings can overwinter inside the natal nest, spending almost a year in the nest before emerging and reaching the wetlands (chapter five). This behavior was observed during three reproductive seasons, with evidence of intra-population variation in this behavior. Hatchlings from some nests overwintered and emerged in spring while hatchlings from other nest emerged in autumn without overwintering in the nest. Although previous research has demonstrated that Australian turtles have several types of delayed emergence responses and adaptations, such as embryonic diapause (Goode and Russell 1968; Kennett *et al.* 1993 a,b; Doody *et al.* 2001), this is the first study to demonstrate hatchling overwintering inside the nest not only in an Australian turtle but also for the entire Chelidae turtle family. Such a finding expands our current knowledge on the diversity of turtles that undertake nest overwintering, as this behavior is described mainly for Northern hemisphere Emydidae turtles (Gibbons 2013). Future investigation should examine whether this is a more widespread phenomenon in *C. longicollis* and other Chelid turtles. Also, a closer look into the proximal (environmental) and ultimate (evolutionary) factors influencing intra-population variation in this behavior would expand our current understanding on the costs and benefits of such dichotomous response. In addition, the present finding of hatchling overwintering inside the nests will be valuable for considering and extending the protection of hatchlings while on land, as they could be impacted by soil management practices and by invasive predators such as foxes (Thompson 1983; Spencer *et al.* 2006) and fire ants (Gibbons *et al.* 2013). Areas under fox control programs should continue year-round where *C. longicollis* have the ability to overwinter inside the nest.

Management implications

The current design of the predator proof-fence in the nature reserve is causing mortality in *C. longicollis* (Ferronato *et al.* 2014). Previous studies have demonstrated the complex habitat use and movements dynamics between permanent and ephemeral waters in *C. longicollis* (Kennett and Georges 1990; Roe and Georges 2007, 2008a,b; Roe *et al.* 2009). In addition, *C. longicollis* abundance is closely connected to its ability to move through the landscape (Kennett and Georges 1990). The fact that the predator-proof fence does not allow for immigrations and completely isolates the fenced turtle population from the wider landscape can have future demographic consequences. The marked propensity for overland movements in *C. longicollis* underscores the importance of landscape connectivity for this species (Roe and Georges 2007, 2008; Roe *et al.* 2009). If no action is taken to allow movements through the fence and mortality continues inside and outside of the fenced enclosure, a decline in the turtle population is expected inside the enclosure over the medium to long-term. Mitigation measures should be applied and the efficacy tested, such as water under-passages along turtle hotspots in the fence, which would allow turtle movements but prevent entry of foxes, cats and rabbits (Ferronato *et al.* 2014). This could help to reduce mortality and permit turtle movements in response to wet-dry cycles (Kennett and Georges 1990; Rees *et al.* 2009). Fence layout should avoid bisecting travel routes among wetlands and also considering distances that turtles seek for terrestrial refugia during droughts (Buhlmann and Gibbons 2001; Ferronato *et al*. 2014). In our system, based on the movement capacity of *C. longicollis*, this should include distant wetlands up to 1.5 km away, which would cover dispersal events and the use of terrestrial refugia (Roe and Georges 2007; Roe *et al.* 2009). It would also be important to continue monitoring the turtle population inside the fenced enclosure over longer periods of time to evaluate their demographic responses to the fence, owing to the potential for both positive (fox removal; Spencer *et al.* 2006) and negative responses (fence mortality, movement disruption; Ferronato *et al.* 2014) over time. Such a long-term study would offer much needed insight into costs and benefits of using such "conservation" fences, considering the scale of potential collateral damage for non-target native wildlife. In addition, assessing whether other conservation fences have a similar disruptive influence on *C. longicollis* populations elsewhere would help to implement mitigation actions that cover the wide range of landscapes and habitats used by *C. longicollis*.

Despite the observation of resilience in *C. longicollis* living in suburban landscapes, I identify hotspots of turtle mortality on roads, with the aid of radio-telemetry – segments of the population that appear to be most vulnerable are those inhabiting small and isolated ponds within the suburbs. Culverts and fencing to direct movements should be used in such circumstances in the city (Dodd *et al.* 2004; Aresco 2005b). In addition, owing to the long distance movements observed here, managers and urban planners should manage contiguous and broad patches of habitat that link suburban systems with surrounding landscapes as a whole rather than as isolated units. A longer-term monitoring of these turtle populations would be essential to the full understanding of turtle dynamics in suburban landscapes over extended time periods.

In conclusion, this thesis helps to cover a range of topics on the ecology, conservation and management of a turtle capable of living in a range of habitats differing in anthropogenic impact, with a longitudinal study to evaluate responses to flood-dry cycles. I was able to demonstrate how these habitats are linked and contribute to the population regulation processes (e.g. migrations, reproduction and mortality) in this freshwater turtle with a remarkable capacity for overland movements. Such examples of population regulation between patches of natural and urban habitats have been mainly described for bird populations (Emlen 1974; Blair 1996; Shochat *et al.* 2006), and I demonstrate that this can also occur in turtles. In addition, I show how the impediment of natural processes such as migrations (e.g. impenetrable fences) can have negative consequences for the demography and conservation of freshwater turtles.

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