Population regulation in snake-necked turtles in northern tropical Australia: modelling turtle population dynamics in support of Aboriginal harvests.

By

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The journey of the turtle spirits

A long time ago, when mainland Australia was connected to islands that now lie off the coast of Northern Australia, ancestral spirits roamed the country. During this time the turtle spirits embarked on a long inland journey from a region known today as the Goulbourn Islands. After many days of travel the spirits began to argue over who would continue on and who would stay. Everyone agreed that some spirits should remain to manage the land that they had already traveled across. After much discussion, which at times was heated, a compromise was struck. The freshwater turtle spirits would continue traveling inland, while the marine turtle spirits would remain and provide custodianship over the region, which today, is inundated by the Arafura Sea. The freshwater turtle spirits realized that the journey ahead would be arduous and at times dangerous. As such, they would have to place an emphasis on being small and inconspicuous to avoid predation, so they offered the marine turtle spirits half of their fat reserves in exchange for traveling no further.

The next stage of the journey crossed over country where water is only seasonally available, causing the legs of some spirits to become so inflamed and their bodies so weak that they could not possibly continue on the expedition. Another discussion was held and it was decided that those spirits (*wamarra* [northern snake-necked turtle]) too weak to travel should remain and survive by storing water under their armpits and burying in the mud to remain cool when waterholes dry. The remaining spirits mustered up the energy to continue inland to the sandstone escarpment. On reaching the large crystal clear permanent billabongs of the escarpment country they realised that they had travelled to where all the local rivers and streams start to flow. As such, it was time for them to go their separate ways and colonise all the rivers of the region.

This story was told to me by Brian Njinawanga Campion (A Rembarrnga speaking elder from Malyanganak) and translated by his son Otto Bulmaniya Campion. It is an extremely important story for people of central and western Arnhem Land because the turtle spirits cross the country of many language groups including *Mawng, Kunbarlang, Kunwinjku, Kune* and *Rembarrnga* on their journey inland. Yellow ochre, collected from cliff faces abutting the sea is used during ceremonies to signify the exchange of fat reserves from the freshwater to the marine turtle spirits.

Dedication

To the people of Arnhem Land and their aspirations - may your land, language and culture remain strong.

Frontispiece: Macy Campion conveying turtle harvest techniques to the children of Buluhkaduru [D. Fordham]

Acknowledgements

I have always had a love of the bush and a strong empathy for the plight of Aboriginal people in contemporary Australia. A desire to travel to Arnhem Land manifested itself at a young age in the back row of a commerce class dreamily flicking through books on northern tropical Australia and its people. After finishing school, my dream was put on hold. I enrolled at university and focused my studies in the disciplines of botany and zoology, ecology and biological anthropology. These studies seeded a strong interest in population dynamics and in particular contemporary wildlife use by indigenous people. Shortly after finishing undergraduate studies, an opportunity arose to assist research projects in Central and Eastern Arnhem Land. This experience reinforced my resolve that commercial wildlife harvesting could benefit Aboriginal people by creating culturally identifiable employment and thereby helping maintain the Aboriginal peoples' strong connection to land and culture. So began seven years working and living amongst the beautiful people of the Maningrida region.

The open hospitality shown to me from Maningrida and outstation residents was moving – there was always a billy on the boil, a friendly smile and room for me to lay down my swag. In particular I thank the outstation communities of Buluhkaduru, Damdam, Jibenna, Kolorbidahdah, Malyanganak, Nanganak and Wurdeja for embracing me and treating me like family. The insight into Aboriginal practices and beliefs that was afforded to me has shaped my outlook on life, heavily influencing my further aspirations. I thank these communities for their trust in granting me access to their traditional lands and for accepting my somewhat peculiar interest in turtles, what locally is viewed primarily women's business. I thank Tommy Steeles from Wurdeja for his painstaking attention to detail when it came to cleaning cooked turtle shells and for his Burrurra language and cultural lessons. The playful battles over preventing my study animals from ending up in the bellies of the Wurdeja community will be the topic of amusement for many years to come. I thank old *Gella* from Malyanganak for showing me the importance of land, culture and the related traditional knowledge. I thank Robert Redford and Charlie Brian from Buluhkaduru, and their respective families, for the open heartedness that was shown to me over the years. I thank Old Joe, Kate, Dean and the Nangank community as a whole for allowing me to establish a home and research laboratory on their lands. Otto Campion has been the inspiration of many of my ideas and I thank him both for his friendship and his knowledge - the world will be a better place if you can achieve half of what you desire for Aboriginal people. Over the course of this study I lost too many good friends at too young an age, owing to the appalling state of Aboriginal health. In particular I thank my brother *Wamud* for his friendship and knowledge and I only hope that I can fill your shoes and follow your footsteps.

I would like to thank my supervisors Prof. Arthur Georges and Prof. Barry Brook for their advice and encouragement and for the complete confidence they afforded in me. Their friendship and enthusiasm in supervision has made my study a pleasure.

I thank the Bawinanga Aboriginal Corporation (BAC) and in particular Ian Munro, David Bond and Jonas Klein for their support. I thank the Djelk rangers for showing me the importance of indigenous resource ownership and management. In particular, I thank Stuart Ankin, Victor Rostran and Russel Brian for helping me initiate the turtle project, and Matthew Ryan and Matthew Hood for their support in later years. I thank the BAC workshop for my mechanical proficiencies.

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socially just environmentally conscious nation.

Finally I would like to thank my parents for their enduring support and encouragement, and for their guidance into a life of research. In particular Sue for her warmth and love, and Adrian for his willingness to have his ear chewed off by my ranting and raving, and for his academic advice and attention to detail. I thank Kiki for her love and patience. I thank Kieran for his help in the field and for his building skills, and Elysha and Kelly for their interest and encouragement.

Abstract

This thesis provides the fundamental science to underpin contemporary harvests of northern snake necked turtles (*Chelodina rugosa*; Ogilby 1890) and their eggs, and presents fresh scientific insights relevant to ecology, conservation and environmental management. Bawinanga Aboriginal Corporation (BAC) recognises that adverse social disruption results from disconnecting indigenous people and communities from their language, culture and traditions. Through sustainable resource utilisation BAC aims to achieve a measure of self-sufficiency for Aboriginal people in the Maningrida region, a continued connection to traditional values and the conservation of natural resources. Wildlife enterprises draw upon land, culture and its related traditional knowledge, creating economically, socially and culturally suitable long-term employment opportunities. Aboriginal people have developed a wealth of knowledge regarding how turtles can be exploited for subsistence without threatening local persistence. BAC is keen to see this knowledge put to use in developing a local industry, focused initially on producing *C. rugosa* hatchlings for the domestic pet turtle market, with a view to expanding to harvests of sub-adult and adult turtles. Here I provide optimal conditions for the storage and incubation of *C. rugosa* eggs and husbandry of subsequent hatchlings, and provide valuable information on the population dynamics of *C. rugosa*, allowing informed decisions on levels of harvest that are biologically sustainable and the offsets that can be put in place to increase harvests.

C. rugosa can nest underwater. My results carry this finding further, by demonstrating that eggs of *C. rugosa* can survive at least 25 weeks inundation, almost six months, with an optimal inundation duration of 6 weeks. Eggs not held under water suffer the same mortality as eggs inundated for 25 weeks, suggesting that underwater nesting is not a facultative capacity but rather, inundation is essential for the optimal survival of embryos. Inundation duration has a profound effect on incubation period, reducing it by up to 9 weeks over what would be expected at a given temperature. I argue that egg inundation is a developmental response to environmental variability in factors that govern timing of reproduction, duration of development and timing of hatching and emergence. Egg preconditioning can be combined with control over incubation and hatching environment to maximize the development and survival of embryos and subsequent hatchlings. Inundation of eggs for 6 weeks (2-10 weeks is acceptable), incubation of embryos at 28°C and raising hatchlings in water at 28°C will yield the best overall outcomes for a hatchling industry.

Many chelonians have low hatchling survival, slow growth, delayed sexual maturity and high sub-adult and adult survival, constraining a quick response to increases in adult mortality from human impacts such as harvesting or habitat alteration. Conversely, *C. rugosa* is fast growing, early maturing and highly fecund relative to many other turtles. Correlative evidence spanning six study sites and three field seasons indicates that *C. rugosa* are somewhat resilient to harvest and pig predation. A decline in sub-adult and adult abundance was correlated with increased recruitment and age-specific fecundity, via enhanced juvenile survival, decreased size at onset of maturity, and increased post-maturity growth. Experimental manipulation of population density of six replicate wild populations of *C. rugosa* confirmed that this species is resilient to negative perturbations in density. Remarkably, in some populations, turtle abundance took as little as one year to recover from a strong negative perturbation (> 50% population reduction) in sub-adult and adult density. Model projections indicate that *C. rugosa* are resistant to chronic increases in mortality. A compensatory decrease in size of female maturity and density dependent hatchling survival are sufficient to allow annual harvests of up to 20 % of sub-adult and adult *C. rugosa* without substantial population suppression. Taken together these results present an open challenge to a universal generality that freshwater turtles are highly susceptible to any form of off-take and that high sub-adult and adult survival is crucial for achieving long-term population stability.

Today pigs (*Sus scrofa*; Linnaeus 1758), an exotic predator, prey heavily on *C. rugosa*, providing an unrelenting predation pressure, compromising subsistence harvest rates and threatening local persistence. Even moderate capture-mark-recapture estimates of pig-related turtle mortality (48 %) exceed what can be accommodated by fast growth, reduced size of maturity and density dependent hatchling survival, leading to severe population decline and extirpation within 30 years. My model projections predict that periodic local culling of pigs, fencing of wetlands to exclude predators, and hatchling

supplementation to off-set losses to predation, are all viable management strategies to ensure ongoing *C. rugosa* harvests.

Collectively, these findings support an Aboriginal industry that aims to achieve economic self-sufficiency and wildlife conservation through culturally identifiable employment.

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Statement of publication and co-authorship

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Statement of contribution

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

- Arthur Georges (Institute for Applied Ecology, University of Canberra) assisted with guidance and general supervision in all aspects of the PhD study including experimental design, data analysis and preparation of manuscripts.

- Barry W. Brooks (Research Institute for Climate Change and Sustainability, School of Earth & Environmental Sciences, University of Adelaide) assisted with guidance and supervision of experimental design, data analysis and preparation of manuscripts.

- Ben Corey (Institute for Applied Ecology, University of Canberra) assisted with field and laboratory work

I as primary supervisor, agree with the above stated proportion of work undertaken for each of the published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Prof Arthur Georges Date

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 “Population regulation in snake-necked turtles in northern tropical Australia: modelling turtle population dynamics in support of Aboriginal harvests”.

I further certify that to the best of my knowledge the thesis contains no material previously published or written by another person except where due reference is made in the text of the thesis.

The material in the thesis has not been the basis of an award of any degree or diploma except where due reference is made in the text of the thesis.

The thesis complies with University requirements for a thesis as set out in http://www.canberra.edu.au/secretariat/goldbook/forms/thesisrqmt.pdf

Damien A. Fordham Date

Prof. Arthur Georges Date

Statement of authority of access

This thesis may be made available for loan. It may be freely copied and distributed for research and teaching purposes.

Damien A. Fordham Date

Chapter 1

General Introduction

Picture: Djelk Rangers trapping gravid *Chelodina rugosa* [D. Fordham]

Indigenous and non-indigenous attitudes towards harvesting wildlife

Harvesting wildlife is a controversial issue. There is overwhelming reticence in non-indigenous societies to exploit native 'higher' vertebrates (e.g. Wilson 1999). On the one hand, the commercial exploitation of native fish and crustaceans is, in general, socially and thus politically acceptable. For example, the Australian Seafood Industry Council reports an annual gross turnover of 2.1 billion dollars (Fitzgerald & Kowalski 2006). On the other hand, there is a widespread view among most non-indigenous people that, ethically, native reptiles, birds and mammals have a right to life that should not be compromised by harvesting. In reality, these are ends of a subjective continuum of species importance where attitudes to harvest are based more on charismatic appeal than strongly held ethical positions or sustainability (Webb 2002).

Conservation groups that rely on public money to operate often promote charismatic wildlife species (viewed in the public eye as 'cute', 'intelligent' or 'friendly') as endangered even when scientific studies show them to be decidedly non-endangered (Bonner 1993a,b). In the case of whaling, the use of ecologically sound arguments by harvesters to demonstrate sustainable resource use has meant that conservation groups that oppose whaling have been forced to argue on the basis of animal rights (Brooch 1993). If society uses farmed exotic animals and their products, it is difficult to argue on moral grounds why abundant native species cannot be exploited, provided that killing and husbandry methods are humane and as long as it poses no threat of population extirpation (Wilson, McNee & Platts 1992). Moreover, the 'free range' harvest of native wildlife is philosophically more defensible on the grounds that the animals are not being taken out of their natural environment and farmed in artificial conditions (Grigg 2002).

Some suggest the need for caveats in regard to the implementation of sustainable harvests (e.g. Robinson 1993), that is harvesting that maintains stable population sizes over the long term. It is argued that as demand increases, owing to increases in human populations or per capita resource consumption, the temptation is to increase harvest supply accordingly (Struthsaker 1998). Although economic, social and political pressures have provided unstainable levels of fish and timber harvesting in some managed populations (Vincent 1992; Ludwig, Hilborn & Walters 1993), sustainable exploitation of a common resource pool is achievable when appropriate management institutions are applied (Ostrom *et al.* 1999).

Despite growing global appreciation of the socioeconomic and environmental benefits of indigenous wildlife use (Freeman 1993; Altman, Bek & Roach 1996; Altman 2003; Altman & Cochrane 2005) and broad acceptance that protectionism alone rarely meets conservation goals (Getz 1999; du Toit, Walker & Campbell 2004), emotionality, subjectivity and political opportunism, rather than rigorous scientific discourse, continues to underlie government decision-making in Australia, constraining indigenous resource access (Webb 2002; Altman & Whitehead 2003). In contrast, countries such as Canada have adopted a far more progressive approach to indigenous resource utilisation (e.g. Fast, Mathias & Banias 2001). The social, economic and cultural costs of blanket opposition to wildlife use is considerable for indigenous people (Wenzell 1991; Freeman 1993), causing *"cultural change that arguably will affect future generations much more profoundly than illness or death caused by infections, carcinomas, substance abuse, or violence"* (Freeman 1997). Furthermore, a policy emphasis on protecting native animals from use, irrespective of sustainability, forgoes a potential to build dynamic conservation approaches that incorporate indigenous resource users to best protect native wildlife (Elmqvist *et al*. 2004).

Socioeconomic, cultural and environmental benefits of indigenous wildlife enterprises

Substantial government funding aimed at improving housing and infrastructure, establishing work based training initiatives and introducing health programs in remote indigenous communities in Australia, has failed to significantly reduce the socioeconomic disadvantage experienced by indigenous Australians (Aboriginal and Torres Straight Islander Social Justice Commissioner 2005; Altman, Biddle & Hunter 2005). Since welfare dependency has, at least to some extent, contributed to the continuing low social standards of remote Aboriginal communities (Pearson 2000), indigenous wildlife enterprise development provides opportunities for socio-economic change through industry creation, by providing tangible benefits at an economic, cultural and environmental level.

Ecologically sustainable development of land and sea resources provides greater economic independence and promotes self-determination among indigenous communities (Robards & Alessa 2004; Altman & Cochrane 2005). Furthermore, commercial wildlife harvests strengthen biological and cultural diversity (Freeman 1993; Collins, Klomp & Birkhead 1996; Gordon & Ayiemba 2003).

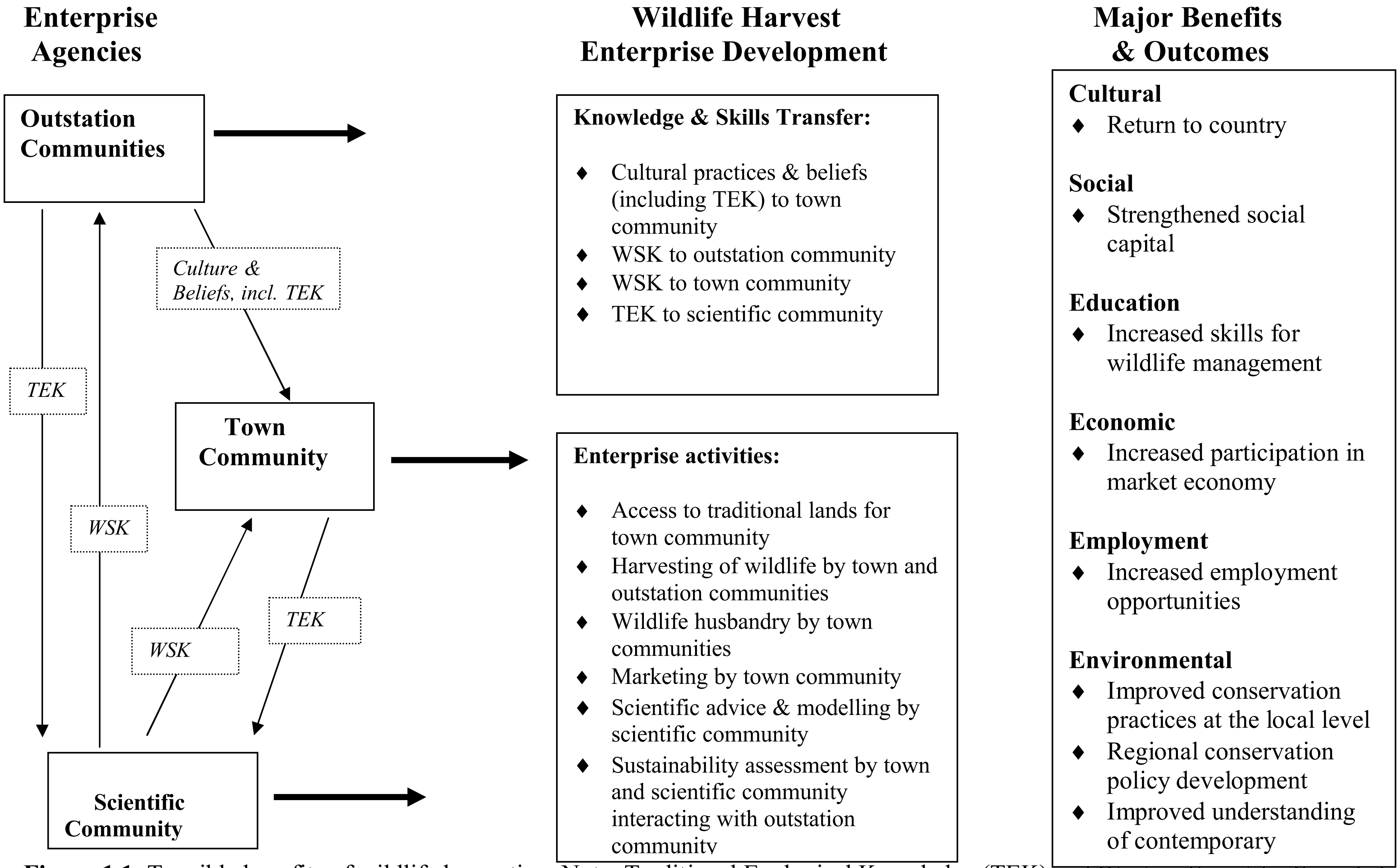
Overexploitation by indigenous and non-indigenous peoples is directly responsible for the precarious conservation status of many species (Jackson *et al*. 2001; Baum *et al*. 2003; Milner-Gulland & Bennett 2003). Nevertheless, if appropriate management practices are implemented, resource utilisation can be sustainable (Brook and Whitehead 2005a,b; Jones *et al*. 2005; Taylor *et al*. 2005). Long-lived organisms display differential vulnerabilities to exploitation (Stevens *et al*. 2000; Fordham, Georges & Brook 2007a), and thus, commercial harvests of wildlife are appropriate in some circumstances, but not in all circumstances (Webb 2002). The important point is that sustainability, or otherwise, determines whether an animal is harvested, not charismatic appeal of certain animals, nor the life stages *per se* that are being targeted (Bonner 1993a,b). Highly fecund, fast growing, early maturing animals with flexible diets and habitats are better equipped to compensate harvests than species that mature late, experience high levels of survival and have long generation times (Shine *et al.* 1998, 1999; Webb, Brook & Shine 2002). Harvesting species with ‘slower’, less flexible life history traits may be sustainable if harvests target life stages that contribute relatively little to population growth (Kokko 2001), such as eggs and juveniles (Gaillard, Festa-Bianchet & Yoccoz 1998). For example, the Maori subsistence harvest of mutton-bird chicks (*Puffinus griseus*) is sustainable (Hunter and Caswell 2002). However, increased mortality of adult birds, resulting from long line commercial fishing, threatens population decline (Hunter and Caswell 2002). Harvesting life stages that contribute heavily to population growth will be sustainable only if highly regulated adaptive management practices are in place, such as for the polar bear (*Ursus maritimus*) under the management agreement for the southern Beaufort Sea (Brower *et al*. 2002).

Over the last quarter of the twentieth century, the indigenous estate in Australia has expanded rapidly in response to land rights and native title legislation. Indigenous Australians control or have management arrangements for some 18% of the Australian continent (Pollack 2001). In the Northern Territory Aboriginal people have exclusive title to around 45% of land and 85% of coastline (Whithead *et al*. 2003). Although indigenous communities, especially in northern and central Australia, tend to be remote from the industry sector (Altman 1990), these perceived losses are set against social, cultural and economic gains associated with residence on Aboriginal land (Taylor 2006). Indigenous lands, especially in northern tropical Australia, are often rich in biodiversity (Yibabuk *et al*. 2001; Brennan *et al*. 2003), and thus, the maintenance of biological diversity in Australia will depend substantially on meeting conservation goals on these lands (Woinarski & Braithwaite 1990). Support for indigenous natural resource use, and in particular wildlife harvesting, has the potential to generate direct economic opportunities in remote indigenous communities with flow-on socio-cultural and environmental benefits (Altman & Whitehead 2003). In short, Aboriginal people contribute significantly to regional conservation efforts by living on and, in turn, managing country. Thus appreciation and support for ecologically sustainable economic opportunities on indigenous lands provide cost effective environmental strategies (Altman 2003).

Isolation from the legacy of poor postcolonial land management practices does not singularly explain high wildlife diversity on indigenous lands in remote areas (Birkhead *et al*. 2000). Rather, a strong indigenous knowledge-practice-belief complex contributes to high biodiversity (Gadgil, Berkes & Folke 1993; Colding & Folke 2001). For example, Aboriginal Australians inherit a spiritual attachment to the land, water and all aspects of their natural environment, sharing a holistic relationship founded on mutual care with that environment (Rose 1984). A close connection between the environment and moral system promotes ‘healthy’ country, *albeit* often inadvertently (Tunbridge 1995), and creates a position where people are less willing to take risks with the environment (Bennett 1983). Furthermore, traditional ecological knowledge is holistic in outlook and adaptive by nature, gathered over generations by observers whose lives depend on this information and its uses (Berkes, Colding & Folke 2000).

Commercial wildlife harvesting strategies can require regular interaction between Aboriginal people in regional centres and Aboriginal people on traditional estates, who partake heavily in customary (subsistence) activities (Fordham, Hall & Georges 2004). This interaction provides a forum that encourages the transfer of cultural knowledge, providing tangible cultural benefits and important environmental outcomes (Figure 1.1). For example, encouraging the conveyance of traditional ecological knowledge potentially strengthens traditional land burning practices, promoting increased biodiversity (Bowman, Whitehead & Walsh 2001; Pardon *et al.* 2003) and reduce smoke emissions, affording environmental and health benefits (Johnston *et al.* 2002; Russel-Smith *et al.* 2003), while concurrently conserving a vital component of Aboriginal culture (Yibabuk *et al.* 2001). What's more, direct conservation outcomes arise from wildlife harvest enterprises that promote access to ancestral estates, creating a frontline for detecting and controlling exotic animals and plants in remote regions of Australia (Altman & Whitehead 2003). In this way, indigenous commercial wildlife enterprises provide an opportunity to conserve biodiversity in regions where conservation is often a priority, enriching biodiversity at a regional scale. Therefore, wildlife harvest enterprises in Australia do not only have a potential to contribute to economic self-sufficiency in remote Aboriginal communities, but also they employ young people in a way that is connected to traditional practices (Webb 1996). By bringing these young people back onto their traditional lands, wildlife harvest enterprises directly and indirectly provide important cultural and environmental outcomes.

Initial uncertainty regarding the sustainability of fledgling commercial harvest enterprises provides an opportunity to formulate effective win-win collaborations between indigenous communities and the government and non-government sectors, potentially creating important advances in education, employment and other socio-economic outcomes for indigenous communities, whilst also meeting conservation goals (Figure 1.1). Training associated with research collaborations that assess sustainable harvests have potential to provide indigenous communities with the skills needed to independently assess and monitor the sustainability of future land management decisions. This is an important step toward resource ownership and, in turn, economic independence and self-determination (Collins *et al.* 1996; Moller *et al.* 2004). Moreover, traditional ecological knowledge is



Knowledge & Skills Transfer:

- Cultural practices & beliefs (including TEK) to town community
- WSK to outstation community
- WSK to town community
- TEK to scientific community

Enterprise activities:

- Access to traditional lands for town community
- Harvesting of wildlife by town and outstation communities
- Wildlife husbandry by town communities
- Marketing by town community
- Scientific advice & modelling by scientific community
- Sustainability assessment by town and scientific community interacting with outstation community

Cultural
- Return to country

Social
- Strengthened social capital

Education
- Increased skills for wildlife management

Economic
- Increased participation in market economy

Employment
- Increased employment opportunities

Environmental
- Improved conservation practices at the local level
- Regional conservation policy development
- Improved understanding of contemporary

Figure 1.1: Tangible benefits of wildlife harvesting. Note: Traditional Ecological Knowledge (TEK) and Western Scientific Knowledge (WSK)

useful in providing information complementary to scientific ecology (Huntington 2000). Thus collaborations provide a forum for traditional ecological knowledge to be acknowledged (Burbidge 1988; Telfer & Garde 2006) and incorporated into regional and national conservation strategies (Barker, Woenne-Green & Mutitjulu Community 1992), contributing to the conservation of biodiversity (Gadgil *et al.* 1993) and ecosystem processes (Whitehead *et al.* 2003).

It is imperative that governments recognise the suite of tangible benefits that underlie wildlife enterprise development and look to the future, providing long-term funding grants that support the training, education and infrastructure costs associated with establishing and implementing wildlife harvest industries in remote localities. In doing so, governments must appreciate that even within apparently homogenous environments, with superficially similar colonial histories, indigenous people are diverse and cannot be treated as a single entity (Turner, Ignace & Ignace 2000). Attitudes among remote Aboriginal communities to the future management of their lands are as varied as they are among non-indigenous Australian communities. They range from those likely to be in direct conflict with conservation objectives, such as negotiating long-term leases over their land for clearing for plantation timber with mutually beneficial profit sharing arrangements (Tiwi Land Council 2003; Firth *et al.* 2006) to uses that are more likely to deliver both socioeconomic and conservation benefits (BAC 2006). In remote communities, with established land access and high biodiversity, wildlife harvest projects will not be all encompassing, but rather, their greatest appeal will extend to people who wish to participate more heavily in customary activities, whilst still maintaining direct attachment to the non-customary sector. Long-term resource access for subsistence and commercial purposes will be fundamental to the social, economic and cultural resilience of indigenous communities (Robards & Alessa 2004). The short-term aims of wildlife enterprise development must be modest, with a focus to the future: a future where economic development in remote indigenous communities is a reality and the conservation benefits of wildlife utilisation attained. This research provides fundamental science to underpin commercial harvests of northern snake-necked turtles (*Chelodina rugosa*; Ogilby 1890) and their eggs in a remote Aboriginal community in northern tropical Australia.

Regional setting

Maningrida Community

My research was conducted in collaboration with the Maningrida community and residents from surrounding outstations (iconic living places on Aboriginal land that are inhabited by usually related, highly mobile indigenous populations; Altman 2006). Maningrida itself is an indigenous community located at the mouth of the Liverpool River in Arnhem Land, a region of northern tropical Australia. The borders of Arnhem Land (a large area of Aboriginal freehold land) extend from the East Alligator River in the west to the Roper River in the south; the coastline marks the northern and eastern boundaries. The area consists of approximately 97 000 km^2 of freehold land under Aboriginal administration. The word Maningrida was derived from the Kunibidji reference to the area, *Mane djang karirra,* meaning the place where the dreaming changed.

The township of Maningrida was established in the late 1940s as a trading post and medical centre to slow the exodus of people from Arnhem Land to Darwin following the Second World War (Hiatt 1965). The Maningrida trading post enabled Aboriginal people to barter cultural artefacts and crocodile skins for western food staples such as flour, sugar and tea. In the 1950s Maningrida became the showplace of the governments new assimilation objectives. A hospital, general store and communal kitchen was built; a cash economy was established employing community members to build roads and houses and establish forestry and fishing enterprises. By the late 1960s most of the Aboriginal people had abandoned their lands in the surrounding region and had moved into Maningrida (Hiatt 1965). During the 1970s the cycle was reversed; people started to move out of Maningrida reoccupying their traditional ancestral estates, in what are now known as outstations, in response to poor living conditions, low employment opportunities and inter-group hostility (Altman 1987). The Australian Labor Party pledged to support Aboriginal land rights as part of its successful 1972 election platform, establishing the Woodward land rights commission, providing grit to the determination of people to decentralise (Meehan & Jones 1980). This social movement was not peculiar to Maningrida (Blanchard 1987) and was significant in that it constituted a rejection of the modernisation paradigm of government settlements and missions and rejuvenation of the customary economy (Altman 2006).

Bawinanga Aboriginal Corporation

The Bawinanga Aboriginal Corporation (BAC) was established in the early 1970s to support people who chose to live on outstations on their traditional clan estates in the 'Maningrida region'. The region is an artificial administrative construct consisting of 10 000 km^2 of tropical savannah in north central Arnhem Land – a region roughly bound by the Mann/Liverpool river catchments to the west, the Blyth/Cadell river catchments to the east and the escarpment to the south (Figure 1.2). As the outstation population has grown to about 800 people on 32 outstations, the corporation's role has expanded. The type of support that the landowners now need goes beyond housing and services. Today BAC continues to operate as a resource agency for outstation residents while facilitating one of Australia's largest Community Development Employment Project (CDEP) schemes (Altman & Cochrane 2005). A key institution within BAC is the Djelk community rangers, supported by CDEP and specific projects funded by the Natural Heritage Trust.

It is widely recognised that adverse social disruption results from disconnecting indigenous people and communities from their language, culture and traditions (Commonwealth of Australia 1997). Accordingly, socioeconomic indicators suggest that there are tangible health and economic benefits associated with outstation living (Altman 2006). BAC recognises this and is responding in a very practical way. It is developing a local economy that will achieve a measure of self-sufficiency for Aboriginal people, a continued connection to traditional values and conservation of natural resources through sustainable utilisation. BAC strives to achieve economic independence and self-determination through the sustainable economic development of land and sea resources (BAC 2006). Economic, cultural and socially appropriate commercial wildlife enterprise development is viewed by BAC as a suitable method for creating meaningful long-term employment opportunities in the Maningrida region, because these enterprises draw upon land, culture and its related traditional knowledge, arguably the greatest assets of the people of this region (Fordham *et al*. 2004).

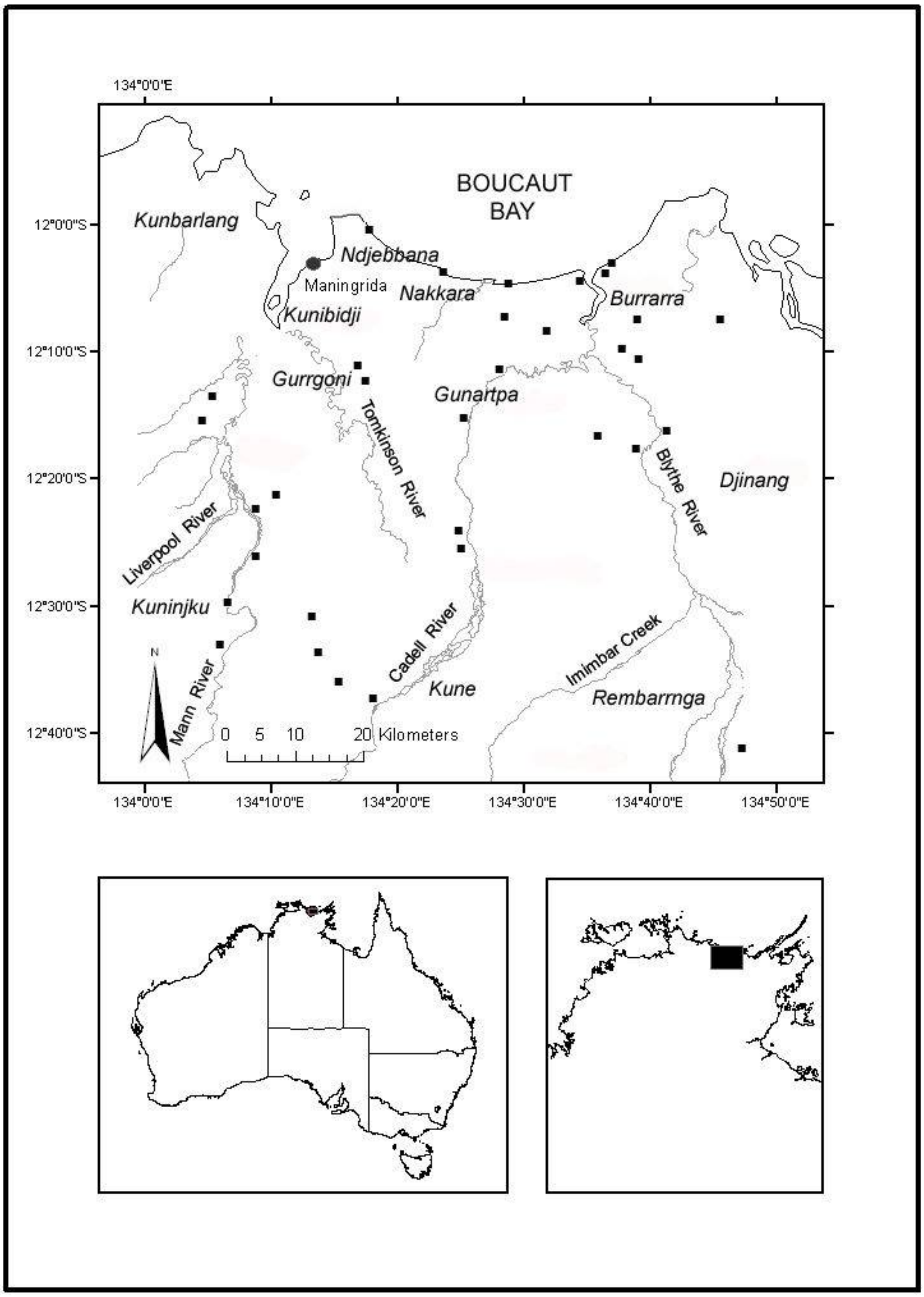


Figure 1.2: The 'Maningrida region' located in northern tropical Australia showing the main rivers, languages (see italics) and outstations (■).

Today ecosystems have been altered to such an extent, through the introduction of feral animals and plants, over-exploitation and land degradation from non-indigenous land uses, that traditional knowledge alone cannot provide the necessary solution to many contemporary land management issues (Barker, Davies & Young 2001; Whitehead *et al.* 2003). Moreover, wildlife harvest enterprises, in themselves, potentially provide yet a further contemporary ecological pressure. BAC, in recognizing the additional effects of contemporary human impacts, distinguishes a need to integrate traditional ecological knowledge with science ecology to best assess the sustainability of potential harvest opportunities. Thus, a fundamental element of the BAC wildlife enterprise model has been collaborations between BAC and key research bodies: namely the Institute for Applied Ecology (IAE) at the University of Canberra, the former Australian Research Council Key Centre for Tropical Wildlife Management (KTWM) and its recent incarnation, the School for Environmental Research (SER) at Charles Darwin University. These partnerships are symbiotic, enhancing biological understanding of harvest stocks and potential harvest rates.

A turtle industry for Maningrida

Freshwater turtles provide Aboriginal people in tropical northern Australia with a significant source of protein (Russell-smith *et al.* 1997; Georges & Kennett 1988). Aboriginal people have developed a wealth of knowledge regarding how turtles can be exploited for subsistence without threatening persistence (Fordham, Georges & Brook 2007d). Harvesting is often bound by strict cultural protocols that define the harvesters, the method of preparation and distribution, the areas and periods in which harvesting can occur and the people that can consume certain species (Altman 1987). BAC is keen to see this knowledge put to use in developing a local industry that contributes to economic self-sufficiency while at the same time maintaining and reinforcing links to Aboriginal culture.

Rock paintings and ceremonial stories indicate that Aboriginal people in northern tropical Australia have been harvesting *Chelodina rugosa* known locally as *wammarra*, *burnda* and *gomdow*, for many millennia (Chaloupka 1993). Methods used to gather *C. rugosa* demonstrate a wealth of knowledge as to the turtle's habitat and life history

(Fordham *et al*. 2006b). For example, at the end of the dry season, dried waterholes and floodplains are burnt to expose the breathing holes of aestivating turtles (Russell-Smith *et al*. 1997). In February 2000, BAC, in collaboration with the IAE and KTWM undertook the first step towards establishing an enterprise focused on the harvest and incubation of *C. rugosa* eggs and the subsequent sale of hatchlings into the pet industry (BAC 2001). This collaboration was established, in part, to guarantee that a shift from a solely subsistence approach to *C. rugosa* utilisation to a commercial approach, including servicing markets beyond Maningrida, did not jeopardise local population persistence of *C. rugosa* or compromise customary harvest rates (Fordham *et al*. 2004).

Turtle harvesting and the issue of sustainable use

Turtles, and their eggs, are commonly harvested for commercial and customary purposes (Clark and Southall 1920; Close and Seigel 1997; van Dijk, Stuart & Rhodin 2000; Frazer 2003; Georges, Guarino & Bito 2006a). Yet turtle harvesting, and in particular the harvest of sub-adult and adults (Heppell 1998) is controversial because it threatens the persistence of many species (Klemens & Thorbjarnarson 1995). The demand for turtle products in Asia is currently met in a large part by the harvest of natural populations at a rate that is unsustainable (Gibbons *et al.* 2000). Many species of freshwater turtle that were once widespread and abundant throughout Asia are now considered locally extinct or regionally endangered as a direct result of over-harvesting for international trade (van Dijk *et al.*, 2000). The mounting crisis, has in part, resulted in a universal perception that ‘slow’ life history traits, combined with fixed demographic parameters, limit the ability of chelonians to spring back after population depression and constrains their ability to respond to a chronic increase in sub-adult and adult mortality, whether it be direct through harvesting, or indirect through habitat alteration (Brooks, Brown & Galbraith 1991; Congdon, Dunham & van Loben Sels 1993, 1994; Doak, Kareiva & Kleptka 1994; Cunnington & Brook 1996; Heppell, Crowder & Crouse 1996a; Heppell *et al.* 1996b; Heppell 1998; Converse, Iverson & Savidge 2005; Spencer & Thompson 2005). Thus harvesting sub-adult and adult turtles is regarded as inherently unsustainable, and therefore unacceptable (Congdon *et al.* 1993, 1994).

Population regulation via compensatory responses occurs through density dependent changes in survival and reproductive success (Rose *et al.* 2001). Density dependent processes appear to regulate population abundance in a diverse range of taxa (Brook & Bradshaw 2006), including long-lived vertebrates (Fowler 1987; Gaillard *et al.* 1998). The very fact that many extant turtle species have persisted despite long histories of harvest, *albeit* with population decline (Parsons 1962; Frazer 2003), suggests that turtles can withstand a level of harvest. Correlative studies indicate that density is compensatory in some turtles (Stubbs *et al*. 1985; Bjorndal, Bolten & Chaloupka 2000; Tiwari *et al*. 2006), though evidence for these conclusions has been limited by (i) the absence of replication; (ii) focus on a compensatory shift in a single demographic parameter rather than assessing all potential compensatory responses; and (iii) the use of indirect evidence of differential survival probabilities rather than direct measures of survival (Fordham *et al*. 2007a). Thus a view towards limiting freshwater turtle harvests because of an apparent absence of density dependent responses continues to prevail (e.g. Reed & Gibbons 2003; Converse *et al.* 2005)

Interaction between population growth and extrinsic factors, such as climatic variability and demographic structure, makes quantifying density dependent responses from field data difficult (Clutton-Brock & Coulson 2002; Festa-Bianchet, Gaillard & Cote 2003). Therefore, I posit that the apparent absence of compensatory regulatory mechanisms reported by Brooks *et al.* (1991b) and reiterated in seminal papers (Congdon *et al*. 1993, 1994) reflects a difficulty in quantifying density dependence in the field, especially considering the long generation times of these freshwater turtle species, rather than an apparent absence of compensatory regulation altogether. It may be that high rates of survival are crucial for some turtle species owing to weak compensatory responses (Cunnington & Brooks 1996; Heppell 1998; Chaloupka 2002), while the life history traits and population dynamics of other species may better equip them to compensate some level of increased mortality through predation or harvest (Fordham *et al*. 2007a; Fordham, Georges & Brook 2007b).

Distribution and taxonomic nomenclature

Chelodina rugosa (Pleurodira: Chelidae) is grouped with other snake-necked turtles in the genus *Chelodina*. The diagnostic features that distinguish the genus are an exceptionally long neck and the presence of only four claws on the webbed front feet (Cogger 2000). *C. rugosa* attains high densities in the ephemeral swamps and other wetlands of the wet-dry tropics of northern Australia from Princess Charlotte Bay in the East to and including the Victoria River in the West (Cogger 2000; Figure 1.3). *C. rugosa* is also found in the Fly delta of New Guinea, from Balimo in Papua New Guinea to at least Merauke in Western Papua (Georges *et al*. 2006a). Throughout this thesis, our study species is referred to as *Chelodina rugosa* (Ogilby, 1890). There is some confusion on this designation because the holotype of *C. oblonga* (Gray, 1841) is a specimen of our study species (Thomson, 2000). The name *C. oblonga* takes precedence. Strictly then, our study species is *C. oblonga*, a name that was applied to it up until 1967. Since then, it has been consistently but erroneously referred to as *C. rugosa*. In the interests of stability of nomenclature, and because an application to conserve current usage of the name *C. rugosa* is before the International Commission for Zoological Nomenclature (ICZN) (Thomson, 2006), *C. rugosa* is used as the name of our study species (Fordham *et al*. 2006b).

Aims and thesis structure

The overarching aims of this research were to (i) provide the necessary scientific underpinning to make judgements on appropriate levels of subsistence and commercial exploitation of *C. rugosa* (eggs and turtles) and to provide practical tools in support of this decision-making; (ii) provide fundamental knowledge and understanding to support the commercial harvest and incubation of *C. rugosa* eggs and subsequent hatchling husbandry; and (iii) capitalise on the opportunity to investigate whether density dependent mechanisms drive a compensatory response to harvest in these long-lived vertebrates. My initial assumption, based on ethnographic records (Russell-Smith *et al*. 1997) was that harvests of *C. rugosa* provide a culturally important seasonal source of protein for communities in Arnhem Land. As such, I expected harvest to constitute the principal source of sub-adult and adult mortality for C. rugosa in Arnhem Land, causing negative perturbations in turtle abundance. However, in undertaking the research, it soon became

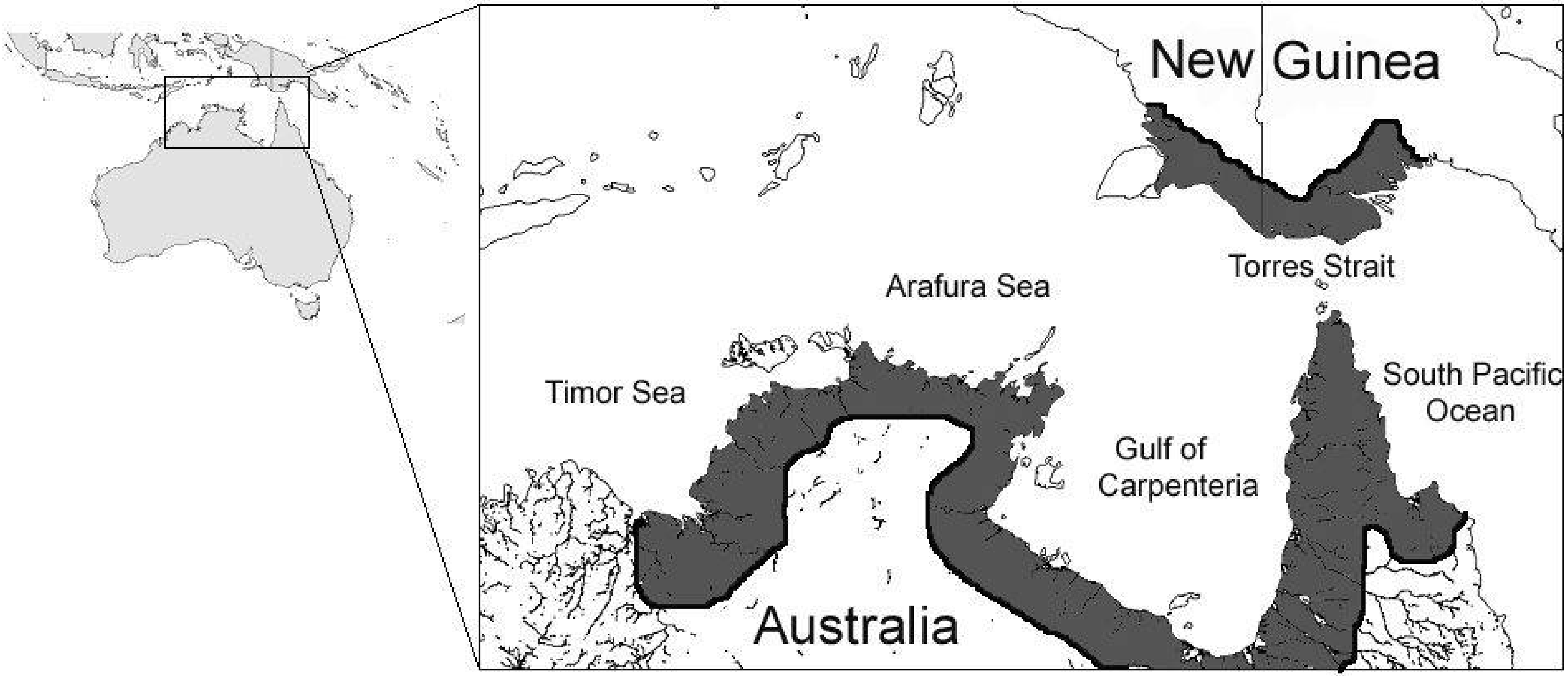


Figure 1.3: *Chelodina rugosa* attains high densities in the ephemeral swamps and other wetlands of tropical northern Australia and the Fly Delta of Papua.

apparent that climatic stochasticity and feral pig predation (*Sus scrofa*; Linnaeus 1758) were major driving factors of turtle survival. The demographic aims were expanded to accommodate these additional variables.

The thesis consists of eight chapters. Chapters 2 and 3 describe a series of experiments that explore the impact of egg inundation duration, incubation temperature and clutch effects on embryonic development, hatchling attributes and egg and hatchling survival and growth. Chapter 2 is presented in the context of life history evolution. Chapter 3 is presented in the context of aquaculture. Chapter 4 describes a radio telemetry study that quantifies survival rates of *C. rugosa* at a traditional turtle harvest site. Chapter 5 and 6 describe experiments to examine whether density dependent processes afford the resilience required for *C. rugosa* populations to recover rapidly from downward displacement of population numbers caused by pig predation and Aboriginal harvesting. Chapter 7 uses predictive models to project the impact of pig predation and harvest (subsistence and commercial) on *C. rugosa* persistence. Chapter 8 provides a synopsis of the research of value to the Maningrida community and other indigenous communities interested in wildlife utilisation, highlighting discoveries of scientific importance. The specific aims of each individual chapter are as follows:

Chapter 2: investigates the influence of duration of inundation-induced diapause, incubation temperature and clutch of origin on embryonic development and survival of *C. rugosa* eggs. Interpretation is placed in the context of considerable environmental stochasticity in factors driving the timing and duration of the nesting period and the timing of hatching and emergence.

Chapter 3: focuses on the influence of duration of inundation, incubation temperature and water temperature on hatchling survival, quality and growth of *C. rugosa* to better inform the Maningrida industry in obtaining hatchling turtles for sale in the domestic Australian pet trade.

Chapter 4: investigates the factors that influence aestivation in *C. rugosa* and identifies the survival cost of aestivation. Focus is placed on detecting whether, and if so, to what extent turtle size, timing of aestivation, aestivation location, or aestivation depth influence survival. An analysis of survival in response to harvest and predation is included, allowing interpretation of the relative impact of contemporary harvest rates on *C. rugosa* populations in Arnhem Land. Turtle survival is discussed against a backdrop of stochasticity in the timing, duration and extent of the seasonal availability of surface water.

Chapter 5: uses correlative analysis to investigate whether the persistence of pig predated and harvested populations of *C. rugosa* are enhanced by compensatory density dependent adjustments in survival, juvenile recruitment, somatic growth, size of maturity and fecundity.

Chapter 6: uses spatial manipulation of population density to examine whether population abundance in *C. rugosa* compensates density displacement. Observed patterns are discussed in light of the general perceptions that turtles do not display density dependent responses and that high sub-adult and adult survival is crucial for achieving long-term population stability in freshwater turtles.

Chapter 7: uses population models to project the impact of pig predation and harvest (subsistence and commercial) on the local persistence of *C. rugosa* in savannah billabongs (water holes) in Arnhem Land. Simulations models are used to explore the relative benefit of management actions, including the viability of headstarting hatchlings to offset predation and harvest.

Chapter 8: draws on each of the proceeding chapters, synthesising research outcomes fundamental to the utilisation of *C. rugosa* and highlighting contributions to advances in science.

The thesis has been written as a series of papers. Other than this introductory chapter and the final synopsis, each chapter has been written as a paper that has been submitted to or accepted by peer-review journals. Thus the thesis unavoidably contains a small degree of repetition in the introduction of some chapters and a variation in citation style, owing to journal requirements. I am the senior author on each paper and was responsible for the experimental design, data collection and analysis, preparation and submission of manuscripts for publication and response to reviewer comments. My supervisors Arthur Georges and Barry Brook assisted in the development of ideas, implementation of the research and writing up of results. Ben Corey provided assistance in the laboratory and in the field sufficient to warrant co-authorship in some papers. Co-authors are listed with the title and reference at the start of each chapter.

Compensation for inundation-induced embryonic diapause in a freshwater turtle: achieving predictability in the face of environmental stochasticity

Picture: Dae Billabong [E. Papageorgiou]

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Summary

We investigated the influence of duration of inundation-induced diapause, incubation temperature and clutch of origin on incubation duration and survivorship of eggs of the snake-necked turtle *Chelodina rugosa* from the wet-dry tropics of northern Australia. Eggs of *C. rugosa* survive at least 25 weeks inundation, almost six months, with a clear optimal inundation duration of 6 weeks. Eggs not held under water suffered the same mortality as eggs inundated for 25 weeks. Underwater nesting is not a facultative capacity but rather, inundation is essential for optimal survivorship of embryos. Inundation duration had a profound effect on incubation period, reducing it by up to 9 weeks over what would be expected for a given temperature. Eggs inundated for up to 7 weeks complete incubation faster than had they been laid at the same time in dry ground. There was remarkable variability in incubation period remaining after correcting for the effect of incubation temperature, inundation duration and clutch. We interpret these traits as adaptations that match the timing and duration of the period available for nesting to the timing and duration of the period available for successful hatching, emergence from the nest and hatchling survival. Our interpretation is placed in the context of considerable environmental stochasticity in the factors driving these variables.

Introduction

Studies of a wide range of oviparous organisms have demonstrated that the incubation period is often greater than the minimum time required to develop from egg to offspring. Perhaps the most extreme cases are in the insect world, where extended periods of diapause, broken in response to a specific environmental cue, effectively uncouple the timing of egglaying from the timing of emergence of the larvae (Powell 1989). In other cases, insects have extended periods of larval life in order to match timing of egglaying and larval emergence to conditions suitable for adult dispersal phase (Jewel Beetle *Buprestis aurulenta*: Linsley 1943). Among vertebrates, many annual fish occupying ephemeral waters cope with unpredictability in the duration of dry seasons by extending the period of development via a series of diapause (Wourms 1972a,b,c), the last terminated by conditions suitable for the survival of the larvae. In amphibians, the duration of the larval period is highly variable within and among species, and is a central characteristic of their life history (Denver 1997). Among amniotes, costs of gestation in mammals and incubation in birds limit the scope for adjustment of developmental times in response to variability in conditions suitable for the offspring, though some birds can adjust development times to ensure synchronous hatching despite staggered laying times (Vinuela 1997; Wiebe, Wiehn & Korpimaki 1998; Both & Visser 2005). Oviparous reptiles are not so constrained since, with notable exceptions (Shine 1988), they deposit their eggs in a nest that they subsequently abandon and have little further direct influence on the fate of their offspring. Morphogenesis can be normal over a range of thermal and hydric environments despite varying rates of development (Ewert 1985; Gutzke & Packard 1987) and an increase in temperature, within bounds, accelerates development (Packard *et al.* 1987; Shine & Harlow 1996; Shine *et al.* 1997b; Georges *et al.* 2005), as does a dry nesting environment (Janzen, Ast & Paukstis 1995). The capacity to vary rates of development through seasonal timing of egglaying (Ewert 1979; Olsson & Shine 1997) and choice of nest site (Cagle *et al.* 1993; Shine, Elphick & Harlow 1997a; Wilson 1998), coupled with embryonic diapause and embryonic aestivation (Webb, Choquenot & Whitehead 1986; Ewert 1991; Ewert & Wilson 1996; Booth 2000) provides reptiles with great scope for adjusting developmental period. Reptiles therefore provide good models for exploring the trade-offs between the potentially competing interests of mother and offspring and the role of control over developmental period in moderating costs of such trade-offs.

From the perspective of the mother, eggs need to be laid at a time dictated by the constraints on accumulation of resources and when seasonal temperatures are conducive to mobilization of those resources for vitellogenesis, ovulation, and the deposition of oviducal contributions to the egg (Ewert 1985). The eggs must be laid at a time when conditions allow nesting activity and when those conditions least compromise survivorship of the mother (Spencer 2002). From the perspective of the offspring, the eggs must be in the nest when conditions are conducive to successful incubation and appropriate developmental outcomes, and they must be laid at a time that allows hatching and emergence from the nest when conditions are suitable for offspring survival and growth (Webb *et al.* 1986; Madsen & Shine 1998). Timing of egglaying and subsequent timing of hatching and emergence are linked by the developmental period. Adjustment of the timing and location of nesting by the mother, in response to natural selection acting upon her survivorship, will potentially result in a shift in the timing of emergence of her offspring. This may in turn compromise the survivorship of the offspring and so her overall fitness. Meeting the needs of these two influences on the mother's overall fitness will require coincident adjustment of the developmental period. So the period during which embryonic development occurs serves not only the purpose of providing sufficient time for the embryo to develop, but provides also coordination between the timing of egglaying and the timing of hatchling emergence in order to maximise overall parental fitness. The developmental period can therefore be expected often to exceed the minimum physiological and developmental requirements for embryonic development.

In this paper, we investigate the influence of duration of inundation-induced diapause (Kennett, Georges & Palmer-Allen 1993b) and incubation temperature on the incubation period of a tropical turtle, *Chelodina rugosa.* This species occupies ephemeral swamps and wetlands of the wet-dry tropics of northern Australia (Kennett 1994). Turtle activity is punctuated each year by the dry season, when the wetlands draw down and often dry completely. The turtles survive this time, which typically ranges from August/September to December/January, buried beneath the ground. The aestivation period spans the season in which most temperate turtle species and many tropical species nest. Female *C. rugosa* nest under water or in highly saturated soils (Kennett, Christian & Bedford 1998) in the late wet season and early dry season, a strategy that allows them to annually lay multiple clutches of eggs prior to aestivation (Kennett 1999). Modification of the vitelline membrane allows oviducal arrest to continue in the form of embryonic diapause while the eggs are inundated (Seymour, Kennett & Christian 1997), and development proceeds only when the soil dries and the hypoxic conditions are removed (Kennett *et al.* 1993b).

The wet-dry tropics of Northern Australia experience extremes of high rainfall during the monsoonal wet seasons and the near absence of rainfall in the intervening dry seasons, coupled with great unpredictability in the quantity that falls and its timing (Taylor & Tulloch 1985; Georges *et al.* 2002).We interpret the influence of inundation-induced diapause and temperature on incubation period in the context of environmental unpredictability in both the period available to turtles for nesting and the period in which conditions are suitable for hatching. For *C. rugosa*, matching optimal timing of egglaying to optimal timing of hatching and emergence, through incubation period as an intermediary, presents a considerable challenge.

Materials and methods

Female *C. rugosa* were collected between May and June 2004 using baited hoop traps set in ephemeral billabongs on the Blyth-Cadel floodplain of Arnhem Land, Northern Territory, Australia. Turtles found to be gravid by palpation were x-rayed to confirm reproductive status and to determine clutch size (after Gibbons & Greene 1979). Turtles carrying 10 or more eggs (n = 25) were shipped by air to the University of Canberra; all other turtles were released at their site of capture. Ten days after capture, each turtle was induced to lay her eggs with an intra-muscular injection of synthetic hormone Oxytocin® at a dosage rate of 1 unit/100g body mass (Ewert & Legler 1978). The turtles were returned to their site of capture and released.

Each egg was labeled with a unique number, weighed (± 0.1 g) and measured (length and width ± 0.1 mm). Ten eggs from each of the 25 clutches were selected at random for allocation to treatments. Pairs of eggs selected at random from each of five of these clutches were systematically allocated to each of five constant temperature treatments (26, 28, 29, 30, 32°C) and each of five inundation treatments (0, 2, 6, 10, 25 weeks) in a Latin Square Design. This basic experiment was replicated four more times using eggs from the remaining 20 clutches. Each replicate was thus based on a total of 50 eggs, and the full experiment was based on 250 eggs. The inundation treatments involved totally immersing the clutches of eggs under water in 250 ml plastic containers fitted with lids that minimised evaporation but did not exclude oxygen exchange between the water and the atmosphere. Inundated eggs were stored in complete darkness at room temperature. Container effects were considered to be negligible, and this effect was incorporated in the clutch effect (eggs were stored as clutches) in subsequent analyses.

Eggs in the 0 weeks treatment were covered immediately after laying with moist vermiculite (four parts water to three parts vermiculite by mass) in 18-compartment plastic boxes fitted with clip-down lids. Each box, with its eggs and vermiculite, was weighed and placed within a Ziploc® plastic bag with a small quantity of water (5 ml). A corner of each bag was snipped to allow air transfer to the eggs. The bags were monitored daily and water was added as required. This ensured a constant 100% humidity level throughout incubation. Each box of eggs was placed in a Thermoline® incubator (Refrigerated Incubator Model RI 170) set at the appropriate temperature. Incubators were not replicated, and incubator effects were kept to a minimum by the use of identical equipment in each treatment. These effects were assumed to be negligible, and differences between incubators are assumed to be in temperature only. Incubation temperatures were monitored daily using thermometers calibrated against a reference thermometer certified as accurate (± 0.1°C) by the National Authority of Testing Agencies (NATA). The incubators maintain temperature using opposing heating and cooling apparatus on a short cycle and are fan forced. Thermal inertia within the chamber was increased by the addition of a 5 litre water container. The incubators maintain constant temperature within an empty chamber of + 0.2°C. Egg containers were rotated within the incubator each time they were inspected. As the remaining eggs completed the inundation phase of their treatment, they were transferred to free compartments in the boxes as outlined above at the appropriate temperature dictated by the experimental design.

Eggs that failed to begin development, that is, eggs that failed to develop a white patch indicating embryonic activity (Thompson 1985), were regarded to have died under inundation. Note that our estimates of survivorship under the inundation treatments (including the control) will include a random element derived from infertile eggs that would have failed to develop whether inundated or not. After an incubation period of 70 days, eggs were checked daily for signs of pipping. Date of pipping was recorded for each egg and taken as the point at which incubation was terminated. Pipped eggs were left in place until hatching was completed. Eggs that developed a white patch but that failed to hatch were counted as having died during incubation. Once eggs had hatched, the compartment into which they were placed was cleaned of vermiculite and fluid, and then partially filled with fresh incubation medium and the hatchling left in place. Hatchlings were checked daily until egg yolk sac had been fully internalised. They were then removed from the incubator, their scutes were notched according to a binary number system, and they were transferred to husbandry experiments.

Data from the Latin Square experiment were analysed to determine the impact of inundation duration, temperature and clutch on incubation period using PROC MIXED in SAS Version 8 (SAS_Institute 2001). Replication of the clutches (5 arbitrary sets, as opposed to blocks) allowed a test of the interaction between inundation duration and temperature. Temperature and period of inundation were treated as fixed factors and clutch was treated as a random factor. The response surface for incubation period as a function of inundation duration and incubation temperature was obtained using a general linear model (PROC GLM) following appropriate transformation (see Results) and examination of residuals. Survivorship during inundation was related to the three factors of inundation duration, temperature and clutch using generalized linear models (PROC GENMOD) with a logistic link function and binomial error structure.

Results

Survivorship

Rates of egg survivorship while under water varied significantly with duration of inundation ($X^2 = 17.5$; df = 4; $P < 0.002$) but not with clutch ($X^2 = 21.1$; df = 24; $P = 0.63$). Survivorship was high at 96-98% for 0, 2 and 6 weeks inundation, declining to 92% at 10 weeks, declining sharply to 78% at 25 weeks.

Rates of survivorship during incubation varied significantly with temperature ($X^2 = 65.26$; df = 4; $P < 0.0001$) and duration of inundation ($X^2 = 20.3$; df = 4; $P < 0.0005$) but not among clutches ($X^2 = 33.4$; df = 24; $P = 0.09$). There was a steady decline in embryo survivorship with increasing temperature, from 80% at 26°C (pooled over clutches and inundation treatments) to 10% at 32°C (Figure 2.1). Survivorship under different inundation treatments (pooled over clutches and temperature treatments) showed a unimodal distribution with mode of 72% at 6 weeks duration dropping to 35% at the

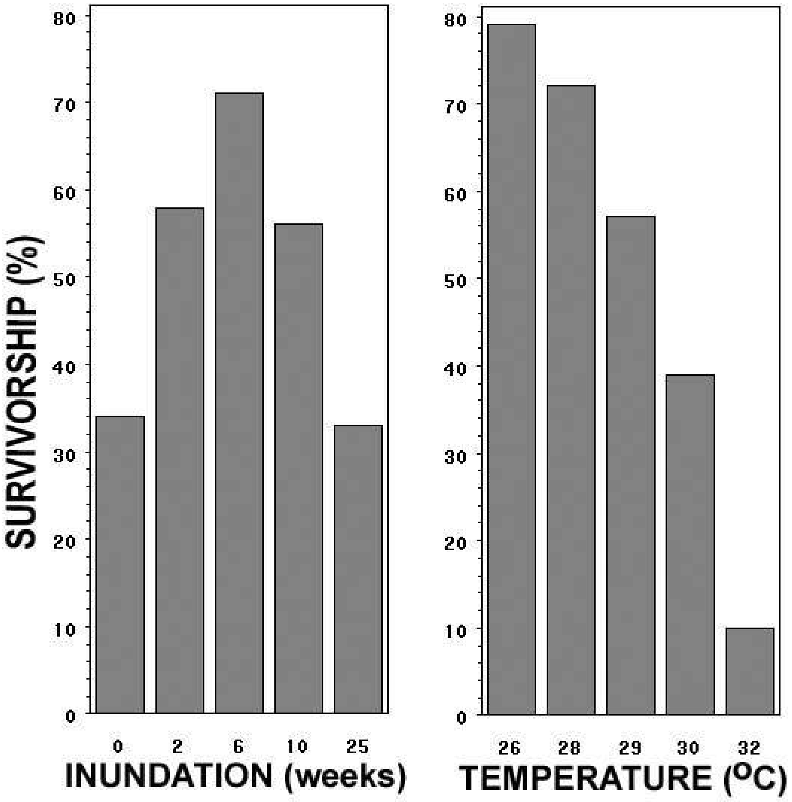


Figure 2.1: Survivorship of embryos of *Chelodina rugosa* to prior egg inundation and incubation temperature. Note that survivorship values for inundation are pooled across temperatures and clutches, and survivorship values for temperature are pooled across inundation treatments and clutches in a Latin Square Design (refer Materials and Methods).

extremes of zero inundation and 25 weeks inundation (Figure 2.1).

Incubation period

Incubation period was profoundly influenced by both incubation temperature ($F = 7.85$; df = 4, 73; $P < 0.0001$) and duration of inundation ($F = 13.27$; df = 4, 73; $P < 0.0001$). There was no interaction between the effects of temperature or inundation ($F = 0.99$; df = 14, 73; $P = 0.48$). The combined effect of temperature and inundation was strong – the expected incubation period of 180 days at 26°C without inundation was 100 days longer than at 32°C and 25 weeks inundation (Figure 2.2). An increase in temperature from 26°C to 32°C decreased incubation period across all inundation treatments, by approximately 40 days, though almost half of this variation could be attributed to change in incubation period in the range 26 to 27°C. Inundation had a stronger effect. An increase in duration of inundation from 0 to 25 weeks resulted in a decrease in incubation period of approximately 60 days, though most of this could be attributed to the first 10 weeks of inundation (Figure 2.2). The equation for the least-squares surface of best fit relating incubation period (*IP*) to inundation duration (*ID*) and incubation temperature (*T*) was

$$IP = 118.0 + \frac{130.90}{ID + 2} - 16.85\sqrt{T - 26} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

$26 \le T \le 32^{O}C$; $0 \le ID \le 25$ weeks; *IP* in days

established by first transforming *ID* and *T* to linear form with an inverse and square root transformation respectively, as indicated in the equation. The proportion of variation in incubation period explained by temperature and inundation duration was 52.8%, without accounting for clutch effects.

There was considerable residual variation in incubation period after the effects of temperature, inundation duration and clutch were removed (variation explained 77.1%), well beyond the few days variation of the synchronous hatching expected of most species of turtle (Booth 1998; Hewavisenthi & Parmenter 2001; Spencer, Thompson & Banks 2001; Ashmore & Janzen 2003). Incubation duration for embryos of *C. rugosa*, after correcting for temperature, period of inundation and clutch, varied about the predictive

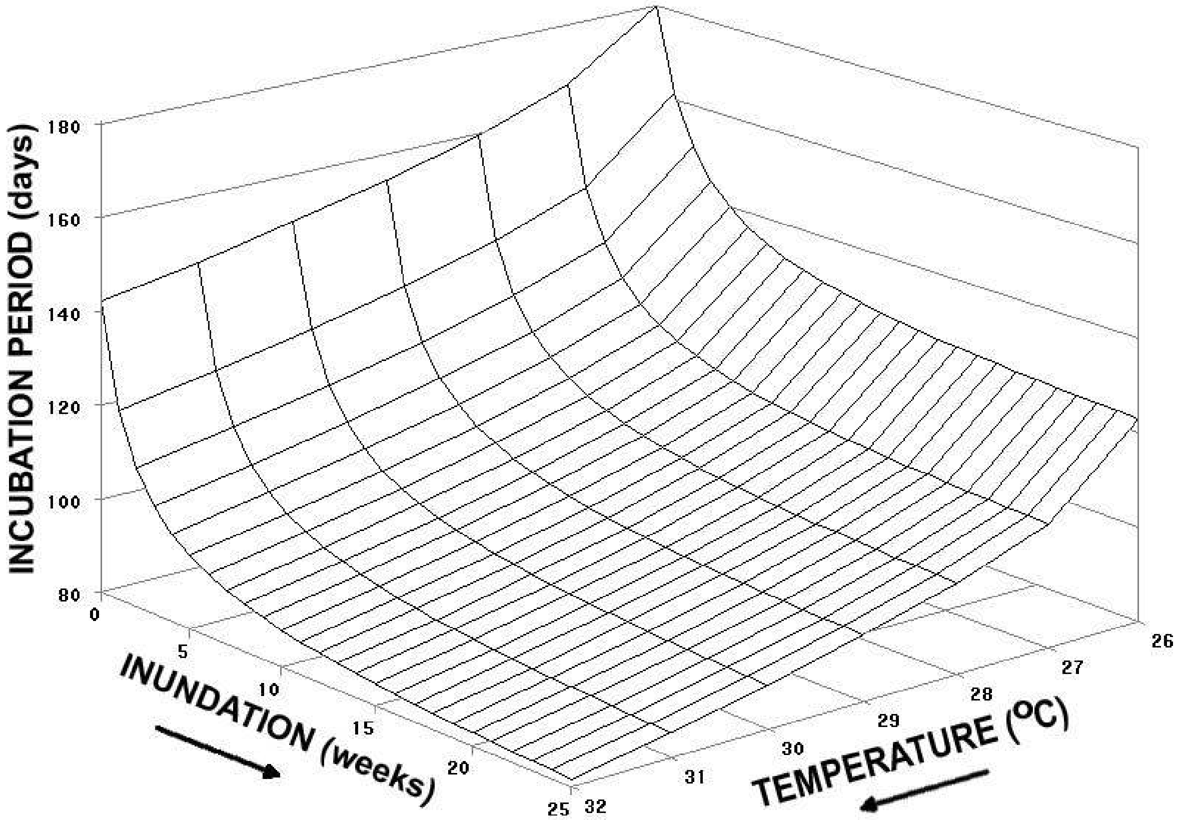


Figure 2.2: Response of incubation period of *Chelodina rugosa* to variation in incubation temperature and inundation duration. Note that incubation period declines with increasing temperature and increasing inundation duration.

relationship by up to 50 days, with a standard deviation of 17.2 days. We lacked an appropriate error term to test the statistical significance of this residual variation, but its magnitude suggests that there are other factors, independent of temperature, inundation duration and clutch, that influence incubation period in this species.

The relationship between incubation and inundation can be expressed in terms of difference in the total time in the ground (inundation-induced diapause plus development time) between inundated and non-inundated eggs to more clearly show the impact of inundation on hatching date (Figure 2.3). Adjustment of development rates in response to inundation compensates entirely for the period of inundation for eggs inundated for up to 7 weeks. Indeed, eggs inundated for 7 weeks or less will be ready to hatch at the same time or before those laid in dry ground. Figure 2.3 also shows a rescaling of the x-axis to units of water depth. This was achieved using the relationship between water depth and time established for Giddadella Billabong (May to September, 2005). These billabongs have a simple pan shaped structure, and water depth decreases linearly through time, as a result of evaporation, evapotranspiration and seepage, at a rate of 2.04 m per annum ($R^2 = 0.9975$). Using this relationship, 7 weeks corresponds to 27.5 cm water depth which, when taking into account core depth of a nest chamber, corresponds to nests laid close to the waters edge and is in close agreement with the depth at which the nests are constructed in the wild (Kennett, Christians & Pritchard 1993a).

Discussion

Our experiments show a number of remarkable results. First, the eggs of *Chelodina rugosa* can survive 25 weeks inundation, almost six months, *albeit* with increased mortality. This is a considerable extension over the open-ended tolerance of 10-12 weeks demonstrated in earlier studies (Kennett *et al.* 1993b; Kennett *et al.* 1998) and is more than adequate to cater for any period of inundation likely to be experienced in the wild. Second, there is a clear optimal inundation duration of 6 weeks, with eggs not held under water suffering the same mortality as eggs inundated for 25 weeks. Previous studies have shown that eggs of *C. rugosa* can survive inundation and can be laid underwater (Kennett *et al.* 1993a). Our result suggests that underwater nesting is not a facultative capacity but rather that

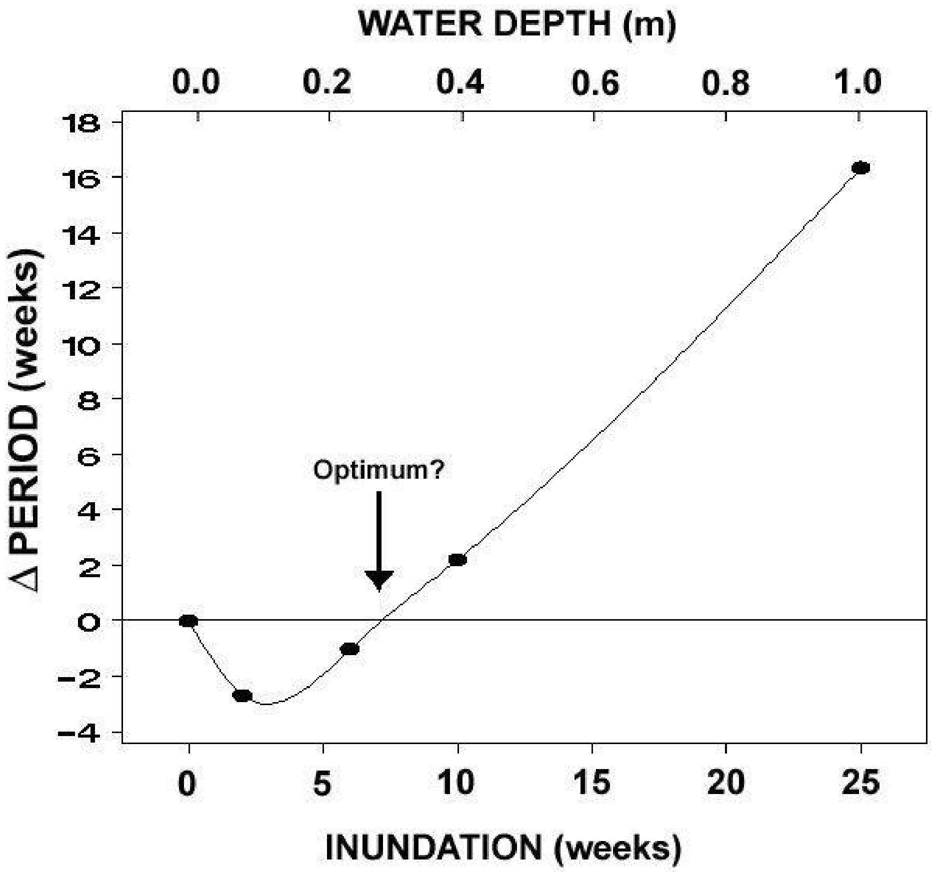


Figure 2.3: Relationship between the change in incubation period (including the period of inundation-induced diapause) and period of inundation for *Chelodina rugosa*. Inundation period is rescaled to water depth based on a relationship describing reduction in water depth with time (2.04 m per annum) for Giddadella Billabong (May to September, 2005). Note that nests that undergo 7 weeks inundation are ready to hatch at the same time as those that are not inundated. This corresponds to the inundation that yields maximum survivorship, and suggests an optimum period of inundation and corresponding laying depth (27.5 cm). If so, and mothers are laying at this depth, nests falling to the right of the optimum are those that have been laid early and subjected to water level rise post-laying.

inundation is essential for optimal survivorship of embryos in this species. Third, inundation duration has a profound effect on incubation period, reducing it by up to 9 weeks over what would be expected for a given temperature. Eggs that are inundated and undergo diapause for up to 7 weeks complete incubation faster than had they been laid at the same time in dry ground. Finally, there is remarkable variability in incubation period remaining after correcting for the effect of incubation temperature, inundation duration and clutch, confirming the results of previous studies on this and closely related species (Beynon 1991).

The challenge is to interpret these new results in the context of the reproductive strategy of *C. rugosa*. To do this we need to characterize the period suitable for egglaying and the period suitable for hatching and emergence, and view the demonstrated influences on developmental time in this context. By nesting underwater, *C. rugosa* is released from the constraint of finding suitable dry land to nest, allowing nesting to begin as early as March, but more typically in April, regardless of the timing and/or intensity of the previous wet season, except in exceptionally dry years when reproduction fails entirely (Fordham, unpublished data). Nesting is terminated by habitat loss when billabongs draw down and turtles prepare to aestivate (Grigg *et al.* 1986; Kennett & Christian 1994), an event that varies considerably in timing from year to year, or in late September, whichever comes first. Thus the timing of egglaying can be viewed as a broad period set intrinsically to fall between April and September, but commonly abbreviated when waters recede and the turtles are forced into aestivation (Figure 2.4). The period suitable for hatching and emergence is the onset of the wet season, when torrential rains soften the soil, allowing hatchling emergence, and fill the billabongs providing hatchlings with habitat necessary for survival. In the wet-dry tropics of northern Australia, the onset of the wet season is a narrow, highly variable window in time. The onset of the rains occurs commonly as early as December and as late as February (Taylor & Tulloch 1985; Georges *et al.* 2002). However, in extreme years turtles may need to be ready to hatch as early as November (Fordham unpublished data). Turtle eggs that fail to complete development prior to the onset of the rains will perish as a result of inundation (Plummer 1976; Webb *et al.* 1983; Kennett *et al.* 1993b). Thus the time suitable for hatching and emergence can be viewed as

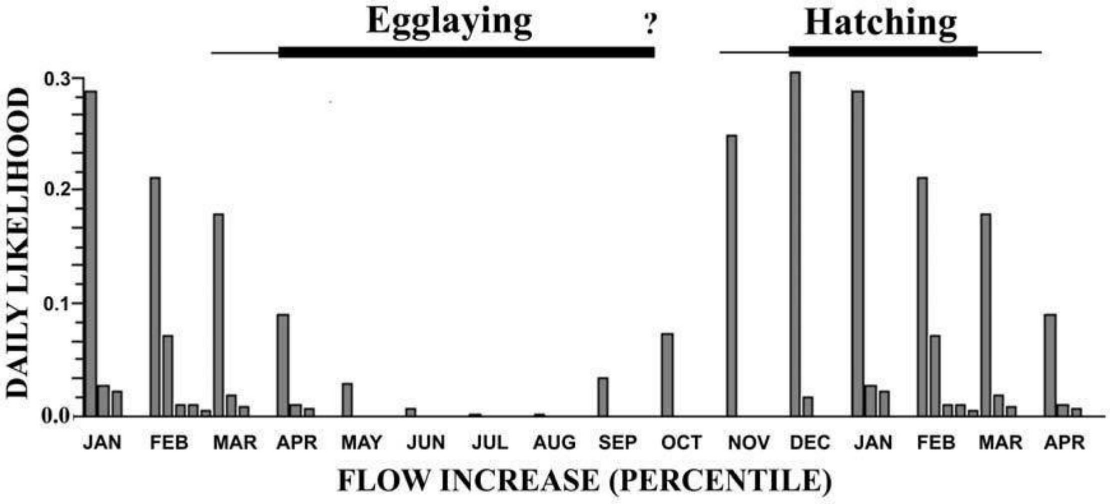


Figure 2.4: Likelihood of daily stage height rises by month calculated from data for Dorisvale gauging station, Daly River, Northern Territory (1960-1998, Station G8140067, data from Georges *et al.* 2002) as an indication of rainfall of sufficient quantity to influence surface water runoff. The horizontal axis is scaled to percentile flow increases by month (columns for each month represent the 10th, 30th, 50th, 70th and 90th percentiles respectively). These data can be used as an index to likely water depth increases across months for areas affected by the monsoonal troughs. Substantial surface flow increases (50th percentile or greater) occur in all months from January to April, with decreasing frequency. Steady water level decline can be anticipated from May to August. Egglaying occurs from early April until late September or until waters recede, whichever is the earliest. Conditions for hatching occur commonly in the months of December to February, rarely in November or March.

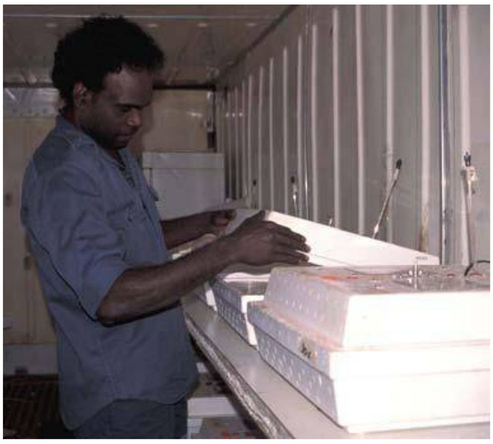
a narrow target moving unpredictably in a 3-month window, December to February (Figure 2.4). We believe that inundation-induced diapause, coupled with the compensatory effects of inundation on development period demonstrated in our study, serves to match the 6-7 month (or less) period of egglaying to the three month period within which conditions suitable for hatching and emergence are likely to occur. Some hypothetical examples serve to illustrate this point. A nest is laid on April 1 in 22 cm of water with a shallow chamber depth of 10 cm (Kennett *et al.* 1993a). A rainfall event, likely at this time of year (Figure 2.4) increases the standing water depth above the nest to 50 cm by May 1, after which water depth decreases in time through evaporation, evapotranspiration and seepage at a rate estimated to be 2.04 m per annum, as judged from the linear decline in water depth for Giddadella Billabong (May to September, 2005). The inundation-induced diapause thus adds 19.6 weeks to the incubation period of eggs laid on April 1. Taking incubation compensation into account (Equation 1) the subsequent incubation period at 26°C will be 124 days. Thus, developmental compensation for inundation shifts hatching date back in time by 59 days bringing the eggs to the point of hatching on December 18. A second nest is laid on June 1, at a water and chamber depth identical to the first nest (a depth of 22 cm and 10 cm respectively). In the absence of rainfall in June (Figure 2.4), water level drops progressively at a rate of 2.04 m per annum (3.9 cm per week), ending the inundation-induced diapause after 8.2 weeks. Subsequent incubation will take 131 days, bringing the eggs to the point of hatching on December 6. Developmental compensation for inundation shifts the hatch date back in time by 53 days. Note that the order of hatching is reversed in comparison with the order of egglaying, so that eggs laid early in the season may well hatch later than eggs laid late in the season. This is a direct consequence of the inundation-induced diapause. Note also that the time interval between the laying dates of these two clutches is 8.7 weeks, but the interval between hatching dates is only 1.7 weeks. A substantial portion of this contraction of hatching period compared to laying period can be attributed to compensation in the incubation period for inundation, in this case 6 days or 12.2%.

Our examples are hypothetical in that we know very little of the incubation temperatures in natural nests (we have set it at an average of 26°C, the optimum for hatching success in our experiment). Variation in incubation temperatures with season, mid-term diapause, delayed hatching after maturation, the unexplained variation in incubation period among eggs, or delay in emergence after hatching may each also contribute to setting the emergence dates of natural nests, and we know little of these aspects of the species biology. However, the examples serve to show that, all other factors held constant, inundation-induced diapause and developmental compensation for inundation can serve to (a) potentially reduce the variation in hatching date compared to the variation in laying date, and (b) shift the mean hatching date back in time - these provide a mechanism for exerting some control over egglaying, development and hatching in the face of environmental stochasticity in the timing, intensity and duration of the monsoonal wet. This reproductive strategy provides potential for complete "folding-over" of hatching times, whereby nests laid early in the season are ready to hatch at the same time as the latest nests of the season. This would commonly occur when clutches laid in March/April experience localized flooding post-laying in an average breeding season. We have demonstrated that *C. rugosa* has sufficient flexibility in its nesting strategy to match the timing of hatching and emergence to the probability distribution for the timing of conditions suitable for hatching and emergence (3 months – December to February), while at the same time, extending its nesting period to the maximum extent (6-7 months, March/April-September).

Chelodina rugosa is not the only freshwater turtle of the wet-dry tropics, and so not the only turtle that must contend with unpredictability in the conditions suitable for egglaying, development and hatching. Rather than nesting underwater, other species occupying ephemeral swamps with seasonally unpredictable water level either seek out the limited opportunities to nest in higher ground (e.g. *Elseya branderhorsti* in the Suki-Aramba swamps of Papua New Guinea) or nest on floating mats that rise and fall with the water level (e.g. *Emydura subglobosa*) (Georges, Guarino & Bito 2006a). The pig-nosed turtle (*Carettochelys insculpta*), a riverine species, lays relatively few clutches, the embryos develop rapidly to maturity before entering embryonic aestivation and hatching is stimulated by hypoxia brought about by torrential rain or flooding (Webb *et al.* 1986; Georges 1992; Doody, Georges & Young 2003). Delayed hatching, in response to an appropriate cue, overcomes variability in the timing of conditions suitable to hatchling emergence and subsequent survival.

Notwithstanding the adaptive responses of other turtle species of the wet-dry tropics, *Chelodina rugosa* shows a diversity of developmental responses to environmental stochasticity usually regarded as the domain of non-amniotes. For example, annual fish of several genera that occupy seasonally ephemeral habitat respond to environmental stochasticity in the timing and duration of dry periods through early anoxic-induced diapause, mid-term diapause and late term embryonic aestivation, the latter terminated by the refilling of their wetland habitat (Wourms 1972a,b,c). This, coupled with high fecundity, ensures their persistence. *C. rugosa* are highly fecund, embryos undergo anoxic-induced diapause, and there are strong indications of a mid-term diapause (Beynon 1991), probably terminated by a cool mid-year chill as in the congener, *C. expansa* (Booth 2002). Hatchling survivorship depends upon emergence that is coincident with resource availability (Van Noordwijk, McCleery & Perrins 1995), so emergence is likely to be delayed until an appropriate cue such as early wet season rains, though this has not been demonstrated. In addition to these developmental responses, *C. rugosa* appear to have a scattergun strategy for coping with unpredictability in the onset of the period suitable for hatchling emergence and survival. A protracted nesting season, during which many clutches are laid by individual females, and embryonic diapause, coupled with high variability in developmental rates among clutches and among eggs within clutches (Beynon 1991), ensures that some eggs will be available to hatch at the onset of the wet season, whether it be early or late. These diverse reproductive traits, comparable to those of some lower vertebrates facing similar environmental challenges (Wourms 1972a,b,c), present *C. rugosa* as possibly a unique amniote model for the study of evolutionary responses to environmental stochasticity in the variables that govern timing of reproduction, duration of development and timing of hatching and emergence.

Optimal conditions for egg storage, incubation and post-hatching growth for the freshwater turtle, *Chelodina rugosa*: Science in support of an indigenous enterprise.



Pictures: *Chelodina rugosa* egg incubation [D. Fordham]

Fordham D, Georges A, Corey B (2007) Optimal conditions for egg storage, incubation and post-hatching growth for the freshwater turtle, *Chelodina rugosa*: Science in support of an indigenous enterprise. *Aquaculture* **in press.**

Summary

Incubation of northern snake-necked turtle (*Chelodina rugosa*) eggs and subsequent sale of hatchlings for the pet industry has the potential to provide culturally suitable employment for indigenous communities in northern Australia. Developmental arrest in response to egg inundation is unique to *C. rugosa*. Eggs can be stored under water for up to 10 weeks without appreciable impact on egg or embryo survival, allowing the transport and sale of eggs into niche markets without high levels of mortality, and permitting eggs to accumulate in diapause until there are sufficient numbers to incubate as batches. Eggs that are not inundated or inundated for short periods experience similar survival rates to eggs inundated for lengthy periods. Incubation temperature influences embryo survival and development period in *C. rugosa*. Embryonic survival is greatest at 26°C, steadily declining as temperature increases to 32°C. A similar increase in incubation temperature decreases incubation period by approximately 40 days, however almost half of this variation is attributed to the increase in incubation temperature from 26 to 28°C. Hatchling growth in *C. rugosa* is characterized by two phases. There is an initial phase of relatively slow growth under the partial influence of initial egg size and incubation duration, followed by a second phase of relatively rapid growth under the partial influence of water temperature and mass at hatching. Post-hatching survival is negatively correlated with duration of egg inundation and water temperature. Evidence suggests that inundation of *C. rugosa* eggs for 6 weeks, incubation of embryos at 28°C and raising hatchlings in 28°C water will yield the best overall outcomes.

Introduction

Production of turtle meat and turtle products is an important component of some local economies in both the developed (Kafuku and Ikenoue, 1983; Hughes, 2000; Lutz, 2000) and developing world (Chen et al., 2000; Sharma and Tisen, 2000; Mai and Tan, 2002). Turtle products are in high demand in Asia (van Dijk and Palasuwan, 2000) driven by the combination of ancient tradition and newfound wealth (Behler, 1997). This demand is currently met in a large part by the harvest of natural populations at a rate that is unsustainable. Many species of freshwater turtle that were once widespread and abundant throughout Asia are now considered locally extinct or regionally endangered as a direct result of over-harvesting for international trade (van Dijk et al., 2000). However, freshwater turtles are also a significant component of aquaculture in many developing countries of the region. For example, China produced 92,000 tonnes of softshell turtle (*Pelodiscus sinensis*) in 2000, primarily for human consumption, equal to 0.6% of their total freshwater aquaculture production in that year (Mai and Tan, 2002). Aquaculture has the potential to mediate the impact of commercial demand for turtle products on wild populations.

In the developed world, demand for freshwater turtles is focused more on their value as pets than on meat or medicinals. A substantial aquaculture industry developed in Louisiana in the late 1950's and by 1969, there were 75 producers and 15 million hatchling red-eared slider turtles (*Trachemys scripta*) passing though the domestic trade (Wood, 1991; Hughes, 2000). In 1975, the US Food and Drug Administration banned domestic sales of turtles less than 10 cm in length in response to concerns over salmonella infections in children (Lutz, 2000). The industry shifted its focus to the international trade in pet turtles (Kuzenski, 1976). In 1996, the United States exported over 8.4 million slider turtles, primarily to Europe and Southeast Asia, representing 85-90% of global trade in pet turtles and establishing the potential for the industry to make a substantial contribution to local economies (Hughes, 2000).

Indigenous communities are showing increasing interest in aquaculture (Skladany et al., 2004), particularly where it has the potential to contribute to the local economy and self-determination. Indigenous enterprises often involve species that have been hunted traditionally, because it is seen to engage young people in activities that connect them with their traditional lands and culture (Webb 1996). In Australia, the Bawinanga Aboriginal Corporation (BAC), representing the indigenous Maningrida community in northern tropical Australia, is keen to develop local industries that contribute to economic independence and self-determination through the sustainable development of their land and sea resources (Altman & Cochrane 2005). A key objective of BAC is to provide employment opportunities for Aboriginal people that draw upon cultural knowledge and provide young people with the prospect to regularly move onto their lands and interact with people that live a more customary (subsistent) lifestyle (Fordham et al., 2004). As part of this initiative, they have established a local industry to produce hatchlings of the distinctive northern snake-necked turtle (*Chelodina rugosa*), initially for the domestic pet turtle market (Fordham et al., 2004), but with an eye to expansion in response to the growing demand for wild meats and natural medicinals, domestically and internationally.

The aim to develop an aquaculture enterprise focused on culturally identifiable employment in part influence the technical challenges of egg collection, incubation and hatchling husbandry. These challenges include (a) obtaining eggs from remote satellite communities (outstations) in sufficient numbers and at an appropriate time to enable them to be incubated in batches; (b) determining the conditions of incubation that optimize egg survival and hatchling viability, and minimize incubation duration; and (c) determining the conditions that are optimal for hatchling survival and growth in preparation for sale.

Chelodina rugosa in many ways lends itself to aquaculture. It is widespread and abundant in the wet-dry tropics of northern Australia (Cogger, 2000), where it lays its eggs underwater during the late wet season at the edge of the waterholes it inhabits (Kennett et al., 1993a). Eggs survive inundation because they have a modified vitelline membrane (Seymour et al., 1997), allowing oviducal arrest to continue in the form of embryonic diapause until the waters recede and the inundation-induced hypoxia ends (Kennett et al., 1993b). Tolerance of immersion in water means that eggs can be readily transported and stored to await incubation. This species is highly fecund compared to other freshwater turtles of a similar size, laying between 6 and 21 eggs per clutch (Kennett, 1999), and 3-4 clutches of eggs per season (Fordham, unpubl. data). Offspring sex of all chelid turtles so far examined is determined genetically (Georges, 1988; Georges and McInnes, 1998). Young turtles grow rapidly, reaching sexual maturity in as little as 4.2 years for males and 7 years for females (Kennett, 1996).

Turtle aquaculture often lacks a solid foundation in science for the collection, incubation and post-hatching husbandry of young turtles, as approaches are often founded in knowledge accumulated in *ad hoc* fashion (Shi and Parham, 2000). In this study, we investigate the influence of duration of inundation, incubation temperature and water temperature on the survival and quality of hatchlings of *C. rugosa* to better inform the Maningrida industry in obtaining hatchling turtles for sale in the domestic Australian pet trade. We show that conditioning of the pre-incubation and incubation environment, not only influences embryological development in *C. rugosa*, but also hatchling fitness and growth. This paper is a continuation of an earlier paper exploring the evolutionary implications of these data on incubation period and egg survival (Fordham et al., 2006).

Materials and methods

Egg Inundation and Incubation

Inundation and incubation procedures are documented in detail elsewhere (Fordham et al., 2006). In summary, eggs were obtained by hormonal induction with Oxytocin® (Troy Laboratories, Smithfield, NSW, Australia) at a dosage rate of 1 unit/100 g body mass (Ewert and Legler, 1978), weighed (± 0.1 g) and labelled with a unique number. Two eggs were selected at random from each of five clutches and systematically allocated to each of five constant temperature treatments (26, 28, 29, 30 and 32°C ± 0.1°C) and five inundation treatments (0, 2, 6, 10 and 25 weeks) in a Latin Square Design. This basic experiment was replicated four more times using eggs from the remaining 20 clutches. The response variables were duration of incubation (time to pipping) and survival rate. Hatchlings were removed from the incubator once their egg yolk sac had been fully internalised. The scutes of each hatchling were notched with a unique number system and they were then transferred to the husbandry experiment.

Husbandry

Hatchlings were grown in one of three Reln 1000 Litre (L) oval water tubs (Reln Plastics Pty Ltd; Ingleburn, NSW, Australia), each with a separate 80 L bio ball filtration system fed by a Pond Master PM-1500 (Kong's [Aust.] Pty. Ltd; Ingleburn, NSW, Australia) submersible pump (flow rate of 1450 L per/hour). Two 48” NEC UV tubes (NEC Lighting, Ltd.), one black tube (emitting 290-320 NM of UVB and 320-400 NM of UVA) and one white tube (emitting 400-700 NM of UV, 280-320 NM of UVB and 320-400 NM of UVA) were suspended 28 cm above the water surface, providing a full spectrum light source. Lights were set on timers to provide a day night cycle. Ultraviolet B exposure during basking is important for endogenous production of vitamin D (Ferguson et al., 2003). Basking platforms constructed from 10 mm thick high-density foam, surrounded by plastic mesh, were available to hatchlings in each tank. Tanks were maintained at a constant water temperature of 26, 28 or 30 ± 0.2°C. Hatchlings were allotted to a water temperature according to egg history, allowing inundation and incubation treatments to be balanced across water temperature treatments. However, the experimental design did not allow for the effects of clutch to be balanced across the husbandry treatments. Water temperature was monitored daily via probes connected to a Datataker 500® series data logger (Esis Pty Ltd; Pennant Hills, NSW, Australia). Probes were calibrated against a reference (± 0.1°C) certified by NATA.

Upon absorption of egg yolk sac, hatchlings were immediately housed in one of three 70 L interim tanks heated at 26, 28 and 30 ± 0.2°C for a standard period of seven days. These tanks were stocked to excess with brine shrimp. Hatchlings were then removed and weighed (± 0.01 g) using a HF-6000 electronic balance (A & D Mercury Pty. Ltd. Seven Hills, NSW, Australia). Maximum straight-line carapace and midline plastron length (± 0.01 mm) were measured using vernier callipers; marks were re-notched where necessary. The hatchlings were then released into grow out tanks. Turtles were fed premium beef mince and vitamin supplements were added to this at a dosage of one tablespoon of Herptivite Multivitamin and one tablespoon of calcium with vitamin D3 (Rep-Cal®; Herp Shop™, Ardeer, VIC, Australia) per kg of mince. A diet of mince was chosen primarily because of its ready availability at low cost in the Maningrida community. Turtles were fed daily to excess and had equal access to food; thus food competition was eliminated. Water fouling was prevented by daily removing uneaten food and by flushing each tank with 200 L of fresh, pre-heated water. Turtle weight and maximum straight-line carapace and midline plastron lengths were measured at weekly intervals. Turtles were removed from the experiment after 26 weeks.

Analysis

Data from the Latin square experiment were analysed to determine the impact of inundation duration, temperature and clutch on incubation period as reported elsewhere (Fordham et al, 2006). The response surface for incubation period as a function of inundation duration and incubation temperature was obtained using a general linear model (PROC GLM) following appropriate transformation. The residuals were calculated for presentation and interpretation in the present paper. Hatchling survival was related to inundation duration, incubation temperature, water temperature and clutch using generalized linear models (PROC GENMOD) in Program SAS Version 8 (SAS_Institute 2001) with a logistic link function and binomial error structure.

Split stick regression (Freund and Littell, 1991) was used to estimate the parameters of two linear segments of the post-hatching growth curve and to identify the junction point K (knot). All other analyses are standard (Sokal and Rohlf, 1995). Means are presented with their standard errors, unless otherwise specified and main effects in the analyses of variance were not interpreted without qualification before first testing for interaction.

Results

Size at Hatching

Hatchlings weighed 7.1 ± 0.1 g on average (3.2 – 10.3 g; $n = 116$) emerging from eggs that initially weighed 14.0 ± 0.2 g on average (7.4 – 21.1 g; $n = 250$). The hatchlings had a mean maximum straight-line carapace length of 33.3 ± 0.25 mm (22.9 – 38.6 mm; $n = 112$) and a midline plastron length of 25.6 ± 0.20 mm (17.7 – 29.2 mm; $n = 112$).

Both incubation temperature ($F = 4.94$; $df = 4, 70$; $p < 0.002$) and clutch of origin ($F = 11.95$; $df = 23, 70$; $p < 0.0001$) had a significant effect on hatchling weight, but the magnitude of the effect in each case was marginal (Figure 3.1). Duration of inundation did

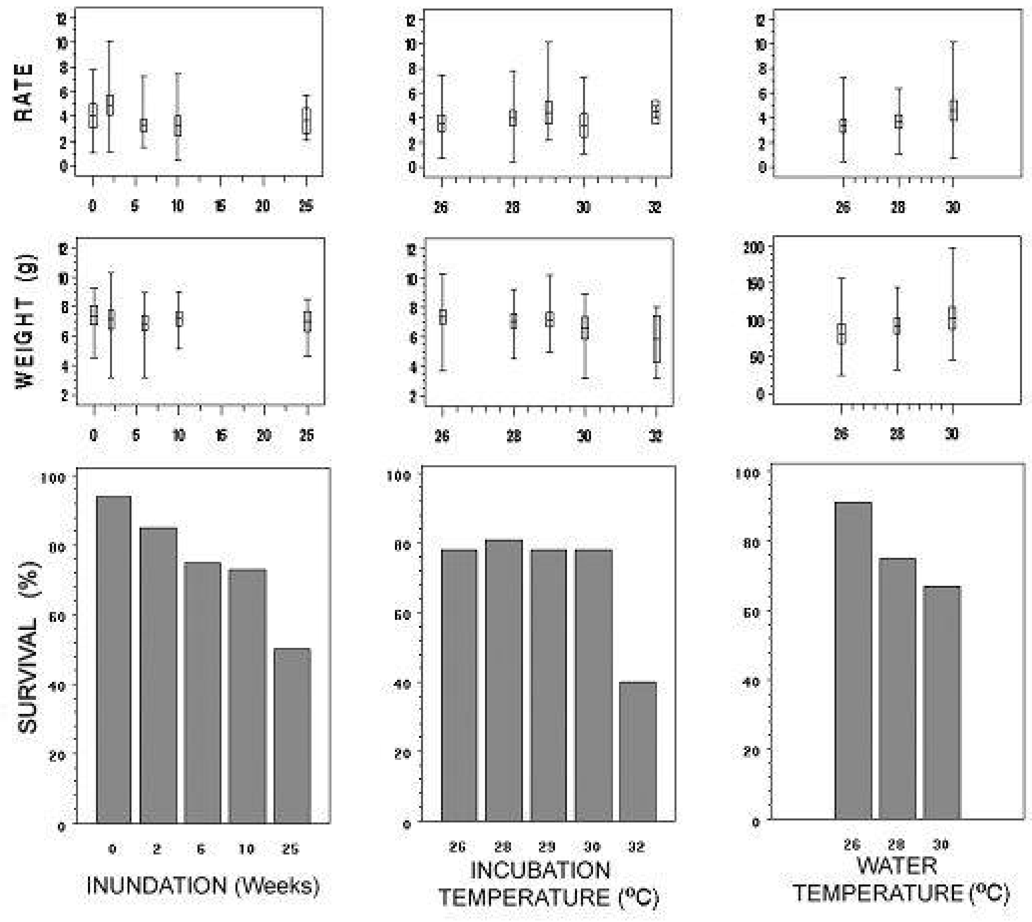


Figure 3.1: Effect of inundation (0, 2, 6, 10, 25 weeks), incubation temperature (26, 28, 29, 30 and 32°C) and water temperature (26, 28, 30°C) on post-hatching survival, initial hatchling weight (final hatchling weight in the case of water temperature) and growth rate post yolk exhaustion.

not have a significant effect on hatchling weight (F = 0.43; df = 4, 70; p = 0.79). By far the most influential variable on hatchling weight was initial egg weight. The two were very strongly positively correlated ($R^2 = 0.72$, F= 286.3; df = 1, 114; $p < 0.0001$). Of the variation explained by this correlation, 88.3% could be explained by clutch of origin. Variation in egg weight among clutches was much greater than variation within clutches. We therefore calculated the predictive relationship between mean hatchling weight (HW) and egg weight (EW) [grams] by clutch using the following equation:

$$\overline{HW} = 0.468\overline{EW} + 0.4 \text{ grams} \qquad (1)$$

($R^2 = 0.81$; F = 95.2; df = 1, 23; $p < 0.0001$)

Post-hatching Survival and Growth

Both period of inundation ($X^2 = 7.93$; df = 1; $p < 0.005$) and water temperature ($X^2 = 6.27$; df = 1; $p < 0.02$) significantly influenced post-hatching survival (Figure 3.1). Highest post-hatching survival occurred in hatchlings that were from eggs that were not inundated or inundated for a relatively short period and housed, following hatching, in the coolest water temperature of 26°C. There was a significant positive relationship between survival and hatchling weight ($X^2 = 14.72$; df = 1; $p < 0.0001$) and this remained significant after correcting for the effect of clutch ($X^2 = 4.04$; df = 1; $p < 0.05$). Incubation temperature did not influence post-hatching survival ($X^2 = 3.55$; df = 4; p = 0.47) though survival at 32°C was extremely low (Figure 3.1).

Post-hatching growth (change in mass) followed a pattern that could be characterised by two distinct segments (Figure 3.2). Growth was at first slow (Phase I growth), then suddenly accelerated to a new higher rate (Phase II growth), which persisted until the end of the experiments. We interpret this as two periods of growth, the first dominated by drawing upon its residual yolk (Phase I), and the second dominated by a period of growth under the influence of food intake (Phase II). The junction point between Phase I to Phase II growth (K, in days) provided an index of the relative duration of each of the two linear segments of the post-hatching growth curve in the 6 months of examination.

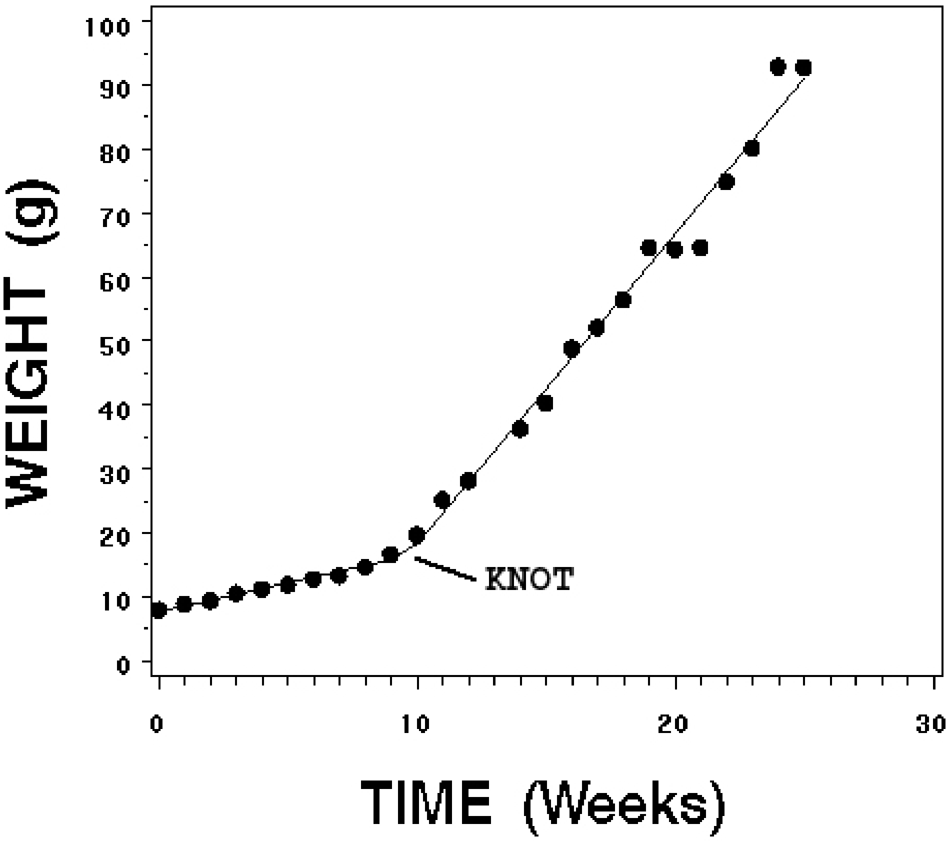


Figure 3.2: Hatchling growth is characterised by two distinguishable segments. Growth during Phase I (left of the knot) is thought to be dominated by utilization of residual yolk. Growth during Phase II (right of the knot) is thought to be dominated by energy derived from feeding (example shows growth for a hatchling reared at 28°C).

Incubation period ($F = 12.87$; $df = 1, 97$; $p = 0.0005$; $R^2 = 0.12$) and egg mass ($F = 8.77$; $df = 1, 96$; $p = 0.0038$; partial $R^2 = 0.07$) were identified as influential on rate of growth in Phase I by a stepwise regression on incubation period, egg mass, duration of inundation, incubation temperature, water temperature and hatchling mass. An increase in either incubation period (decrease in development rate in the egg) or an increase in egg mass results in a marginal increase in the rate of early post-hatching growth. Incubation period was also weakly influential on parameter K ($F = 4.93$; $df = 1, 98$; $p < 0.05$; $R^2 = 0.04$), which determines the duration of the early phase of growth. An increase in incubation period (decrease in embryonic development rate) would be expected to prolong early post-hatching Phase I growth.

Post-hatching growth after the initial phase of relatively slow growth was positively influenced by water temperature ($F = 7.94$; $df = 1, 98$; $p < 0.01$; $R^2 = 0.08$) and mass at hatching ($F = 6.57$; $df = 1, 97$; $p < 0.02$; partial $R^2 = 0.05$). Final size of hatchlings raised in 30°C water (102.4 ± 7.46 g; 46 – 198 g) was 25.2% greater on average than those raised in 26°C water (81.8 ± 6.42 g; 25 – 156 g).

Discussion

This research emerged from the desire of the Bawinanga Aboriginal Corporation to develop an indigenous enterprise initially focused on egg harvesting for the production and sale of hatchling turtles, with a view to expanding to rearing turtles for meat and medicinal purposes. Egg harvesting focuses on the least sensitive stage class for population growth (Cunnington and Brooks, 1996; Heppell, 1998), and as such, egg harvesting provides little threat to population persistence. The optimal conditions for the storage of eggs, their incubation, and the subsequent growth of hatchlings requires integration of previously studied data with those presented in this paper.

Eggs of *C. rugosa* can withstand extended periods of hypoxia through inundation, up to 10 weeks without suffering appreciable mortality, and an overall tolerance of 25 weeks (Fordham et al. 2006). Developmental arrest in response to hypoxia in *C. rugosa* carries with it a number of unique advantages for the industry. The ability to store eggs immediately after laying for up to 10 weeks without appreciable impact on egg or embryo survival permits egg transportation (under water) without incurring high levels of mortality similar to those reported during the transport of eggs of other turtle species (Harry and Limpus, 1989; Parmenter, 1980). Six weeks inundation actually improves embryonic survival compared to no inundation (Fordham et al., 2006). This unique feature of the biology of *C. rugosa* opens up potential niche markets such as that provided by research laboratories nationally or internationally for eggs of this species, but perhaps more importantly, it allows the accumulation of eggs in diapause until there are sufficient numbers to incubate as a batch. A window of 2-10 weeks inundation is sufficiently broad to allow the accumulation of eggs without a marked cost in egg survival.

Embryonic survival, developmental period and size at hatching are often influenced by incubation temperature (Booth, 2000; Brooks et al., 1991a; Georges et al., 2005; Hewavisenthi and Parmenter, 2001; Reece et al., 2002). An increase in incubation temperature, within bounds, accelerates development without adversely affecting morphogenesis (Ewert, 1985), so the optimal temperature for incubation is a trade off between maximizing hatching success, minimizing incubation period and possibly maximizing hatchling size. Fordham et al. (2006) found that embryonic survival of *C. rugosa* was greatest at 26°C, steadily declining as temperature increased to 32°C (Figure 3.3). Similarly, an increase in incubation temperature decreased incubation period by approximately 40 days; however almost half of this variation in incubation period could be attributed to the increase in incubation temperature from 26 to 28°C. These results suggest that 28°C would be a good compromise to ensure both high survival of the embryos and a relatively short incubation period (Figure 3.3). The effect of incubation temperature on size at hatching was marginal, it being dominated by initial egg size.

The high variability in incubation period observed in *C. rugosa* at a given inundation and incubation regime is rare amongst turtles, hatching tending to be synchronous (Booth, 1998; Hewavisenthi and Parmenter, 2001; Spencer et al., 2001; Ashmore and Janzen, 2003). Our analysis of residual variance (Figure 3.3) showed variation in hatching time of ± 50 days for eggs treated in the same way. When incubated

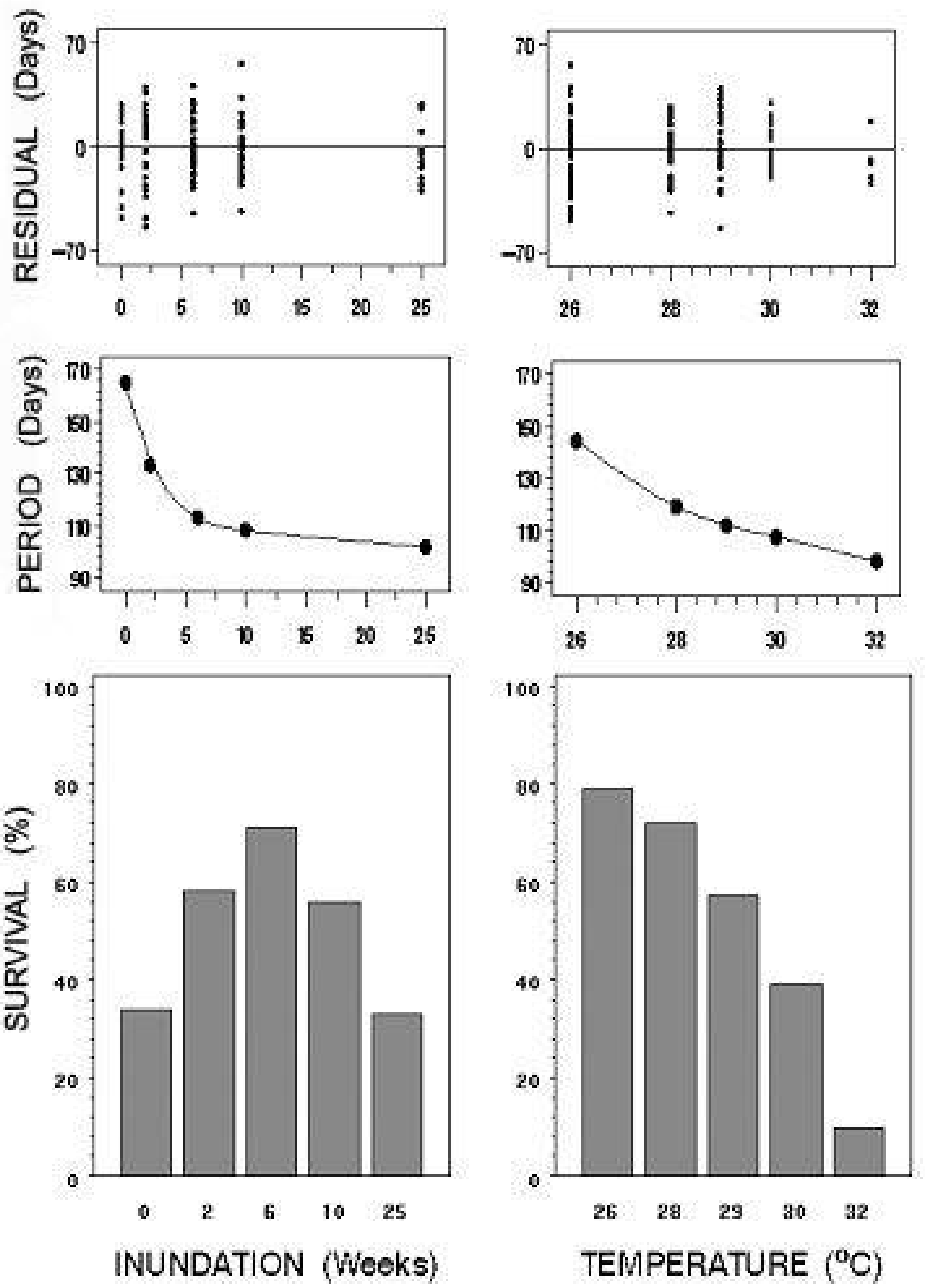


Figure 3.3: Effect of inundation (0, 2, 6, 10, 25 weeks) and incubation temperature (26, 28, 29, 30 and 32°C) on egg survival, incubation period and residual variation among eggs in incubation period (after Fordham et al., 2006). Incubation period is plotted as the marginal means from the Latin Square ANOVA, noting that the inundation and associated temperature effects were additive (Fordham et al., 2006). The residual variation in incubation period as shown is after the effects of temperature, inundation and clutch have been removed.

as a batch, this variation greatly increases the duration of attention the eggs need, with consequential inefficiency. It is not known whether this high variability is a feature of the life history of *C. rugosa* to cope with unpredictability in the onset of conditions suitable for hatching in the wet-dry tropics (Fordham et al., 2006), or whether, in addition to inundation induced diapause, there is some form of mid-term diapause or late-term embryonic aestivation that has not been taken into account. A mid-term diapause terminated by some environmental cue such as a low temperature pulse (as occurs in *Chelodina expansa*; Booth, 2002), or late term embryonic aestivation terminated by increased moisture (as occurs in *Carettochelys insculpta*; Webb et al., 1986), would serve to entrain embryonic development and reduce variability in hatching times for eggs inundated and incubated under identical conditions. The existence, or otherwise, of additional periods of embryonic diapause or aestivation during the embryonic development of *C. rugosa* awaits further research.

Our research confirms the findings of other studies of turtles (Finkler, 1999) and other reptiles (Hare et al., 2004) in demonstrating an effect of incubation environment on post-hatching survival. Post-hatching survival of *C. rugosa* was negatively correlated with duration of inundation (Figure 3.1). Calcium is leached from the shell during egg immersion in *C. rugosa* (Seymour et al., 1997). Since the eggshell provides a substantial source of calcium for hatchling reptiles (Packard et al., 1992; Shadrix et al., 1994), the negative relationship between hatchling survival and egg immersion may reflect a cost associated with calcium leaching during inundation. Incubation temperature did not appear to influence post-hatching survival, though the survival of hatchlings that emerged from eggs incubated above 32°C was very low (Figure 3.1).

Hatchling growth in *C. rugosa* is characterized by two phases (Figure 3.2). There is an initial phase of relatively slow growth under the partial influence of initial egg size and incubation duration (or correlates), followed by a second phase of relatively rapid growth under the partial influence of water temperature and mass at hatching (or correlates). This pattern was adequately modelled for the six-month period of this study by a regression comprising two linear segments. The timing of the switch from Phase I to Phase II growth varied from hatchling to hatchling and was weakly correlated with incubation duration. Residual egg yolk is important in meeting the initial metabolic demands of hatchling reptiles (Kraemar and Bennett, 1981; Webb et al., 1986; Whitehead, 1990). We suggest that Phase I growth is dominated by the period in which residual yolk, absorbed as a yolk parcel into the body cavity shortly before or after hatching, is used to sustain growth. We showed that an increase in either incubation period (decrease in development rate in the egg) or an increase in egg mass resulted in a marginal increase in the rate of early post-hatching growth. Incubation period reflects overall rate of development within the egg, which is likely to affect anabolic efficiency (Booth et al., 2000). Egg mass is likely to be related to initial yolk mass (Packard et al., 1987). Hence, the two variables that have been identified in our analysis as being related to early hatchling growth also potentially influence the amount of residual yolk available to the hatchling. This is consistent with the above suggestion that the dominant influence on rate of growth soon after hatching is that of residual yolk.

We interpret Phase II growth as representing the period after the internalized yolk is exhausted when the hatchling is actively feeding and where growth rate is primarily under the influence of food uptake. Other studies have shown that hatchling size (Valenzuela, 2001), incubation environment (Rhen and Lang, 1995; Roosenburg and Kelly, 1996; Du and Ji, 2003; Ji et al., 2003) and maternal identity (Brooks et al., 1991a; Bobyn and Brooks, 1994; Steyermark and Spotila, 2001) can influence hatchling turtle growth. In our study, water temperature had the greatest influence on hatchling mass at 6 months. Hatchlings raised in 30°C water tend to be 25.2% heavier on average than those raised at 26°C, indicating that the higher temperature is more suitable for maintaining hatchling *C. rugosa*. This conclusion needs to be qualified by the reduced survival of hatchlings with increasing water temperature (Figure 3.1), suggesting that rapid growth in *C. rugosa* may have associated costs (Forsman, 1993; Sorci et al., 1996; Warner and Andrews, 2002).

Conclusion

Integrating results of our experiments (Table 3.1) suggests that inundation of eggs for 6 weeks (2-10 weeks is acceptable), incubation of embryos at 28°C and raising hatchlings in 28°C water will yield the best overall outcomes. A trade-off exists between hatchling survival (highest at water temperature of 26°C) and hatchling growth (greatest at 30°C), somewhat limiting the possibility of industry expansion to the rearing of turtles for food. Further attention should be paid to increasing hatchling survival at 30°C to achieve both high survival and the highest rates of growth. This, together with the issue of entraining embryonic development to achieve a short and predictable incubation period, await further research.

Table 3.1: Summary of the responses to duration of inundation, incubation temperature and water temperature. Inundation of eggs for 6 weeks, incubation of embryos at 28°C and raising hatchlings at a water temperature of 28°C will yield the best overall outcomes, though trade-offs are required between incubation period versus embryo survival, and hatchling growth and survival.

Criterion	Duration of Inundation					Incubation Temperature					Water Temperature		
	0	2	6	10	25	26	28	29	30	32	26	28	30
Egg survivorship	▓	▓	▓	▓	░								
Embryo survivorship	░	▨	▓	▨	░	▓	▨	░	░	░			
Hatchling survivorship	▓	▨	▨	▨	░	▓	▓	▓	▓	░	▓	▨	░
Overall		▨	▓	▨		▓	▨				▓	▨	
Embryo growth	░	▨	▓	▓	▓	░	▨	▨	▨	▓			
Hacthling growth	▓	▓	▓	▓	▓	▓	▓	▓	▓	░	░	▨	▓
Overall		▨	▓	▓	▓		▓					▨	▓
Combined assessment		▨	▓	▨			▓					▓	

▓ Optimum ▨ Acceptable ░ Unacceptable

Feral pig predation threatens the indigenous harvest and local persistence of snake-necked turtles in northern Australia.

Picture: Feral Pig [Invasive Animals CRC]

Published as: Fordham, D., Georges, A., Corey, B. & Brook, B.W. (2006) Feral pig predation threatens the indigenous harvest and local persistence of snake-necked turtles in northern Australia. *Biological Conservation*, 133, 379-388.

Summary

Northern snake-necked turtles (*Chelodina rugosa*) traditionally provided an important seasonal source of protein for indigenous communities in Arnhem Land, northern Australia. Harvest techniques today differ little from those used historically, harvesting being applied in the late dry season when ephemeral waters have drawn down and turtles are aestivating. Radio-telemetry was used to quantify survival rates of C. rugosa at a traditional turtle harvest site and relate them to harvest, predation by feral pigs (*Sus scrofa*) and environmental factors. Although turtle survival was positively correlated with body size, the survival of turtles of all sizes and stages of maturity was compromised by pig predation. Seasonal variation in the onset, duration and severity of rainfall and associated influences on periodic drying, are important for C. rugosa survival because such variation influences the timing and intensity of both Aboriginal harvest and pig predation. Contemporary harvest rates of C. rugosa in Arnhem Land by Aboriginal people are very low because pig predation depletes available stocks immediately before Aboriginal harvesting. Aboriginal harvest rates are regulated also by the frequency and timing of ceremonies and other cultural activities that interfere with harvests. Before the arrival of pigs, such relaxation of harvest pressure in years when it would otherwise be possible would have contributed to the local abundance and persistence of C. rugosa. In contrast, pig predation is unrelenting, and years of high turtle survival are now restricted only to years of high wet season rainfall.

Introduction

High adult survivorship is viewed as crucial for achieving long-term population stability in turtles (Crouse et al., 1987; Heppell, 1998; Congdon et al., 2001). Mark-recapture studies demonstrate that turtles tend to have life history strategies characterised by low juvenile survivorship, delayed maturity and high adult survivorship (Brooks et al., 1991b; Congdon et al., 1993, 1994). Since a small reduction in adult survivorship over time can lead to population decline in some species (Heppell and Crowder, 1996; Spencer and Thompson, 2005), human-induced changes resulting in depressed adult survivorship are of great concern (Garber and Burger, 1995; Heppell et al., 1996; Close and Seigel, 1997; Galbraith et al., 1997; Hall et al., 1999; Aiken et al., 2001; Gibbons et al., 2001). However, the life history traits and population dynamics of some turtle species may be better equipped to compensate for relatively low rates of adult survivorship than other species (Kennett, 1996, 1999; Webb et al., 2002). Reptiles that rely upon fast growth rates, a low age at onset of maturity and high fecundity can persist under conditions of relatively low adult survivorship (Fitzgerald, 1994; Shine et al., 1998, 1999). Furthermore, some turtle species may partially compensate for decreased adult survivorship through density dependent responses (Stubbs et al., 1985; Kennett, 1994; Bjorndal et al., 2000).

The northern snake-necked turtle (*Chelodina rugosa; Chelidae)* is fast growing, early maturing and highly fecund in comparison with other turtles (Kennett, 1994). It attains high densities in ephemeral swamps and other ephemeral wetlands of the wet-dry tropics of northern Australia. As such, it experiences the extremes of high rainfall during the monsoonal wet seasons and the near absence of rainfall in the intervening dry seasons. Turtle activity is punctuated each year by the dry season, when the wetlands "draw down" and often completely dry. Turtles survive desiccation during the dry season, typically from August/September to December/January, by burying themselves beneath the ground and aestivating (Kennett and Christian, 1994). Towards the end of the dry season aestivating *C. rugosa* provide a potential source of protein for indigenous communities living on, or near, flood plain environments (Russel-Smith et al., 1997). Women are the primary harvesters of *C. rugosa*. Rainfall in the wet-dry tropics is highly variable both within and across years in the quantity that falls and its timing (Taylor and Tulloch 1985; Georges et al., 2003). In unusually wet years billabongs do not dry, turtles do not aestivate, and turtle harvesting is limited (Fordham, unpublished data). Accordingly, the harvest of *C. rugosa* is not necessarily an annual event.

Contemporary harvest rates of *C. rugosa* have declined at billabongs that traditionally were sites of heavy harvest (Barker, 1993). This may be a result of increasing feral pig (*Sus scrofa*), buffalo (*Bubalus bubalis*) and cattle (*Bos taurus*) densities on indigenous lands, with consequent damage to habitats, and potential direct effects of trampling on aestivating turtles and predation on nests and adults (Barker, 1993; Robinson et al., 2005). Pigs, buffalo and cattle have a devastating impact on ephemeral wetlands in northern Australia (Bowman and Panton, 1991; Mulrennan and Woodroffe, 1998). There is no evidence that declining harvest rates are the legacy of cultural transformation to meet contemporary requirements (Barker, 1993). As such, observed declines in turtle harvest returns for effort and overall yields are of a cultural concern to Aboriginal people because customary harvesting and the preparation of traditional foods are important for cultural expression, providing a vital avenue for the generational transfer of cultural knowledge (Altman et al., 1996; Freeman, 1997).

As such, distinguishing the cause of harvest decline of *C. rugosa* is of importance from a cultural as well as a management and conservation perspective. To date, the question of whether reduced harvest rates reflect a regional decline in *C. rugosa* population densities, interference with harvest methods by increased levels of feral animal disturbance at ephemeral billabongs, or a combination of these factors has not been addressed. In addressing this question, this paper assesses what factors influence aestivation in *C. rugosa* and identifies the survival cost of aestivation. Radio-telemetry was used to determine whether survivorship is continuous or punctuated by periodic drying. Focus is placed on detecting whether and to what extent turtle size, timing of aestivation, aestivation location, or aestivation depth influences survivorship. An analysis of survival in response to harvest and predation is included, allowing interpretation of the relative impact of contemporary harvest rates on *C. rugosa* populations in Arnhem Land. These findings are discussed against a backdrop of stochasticity in the timing, duration and extent of the seasonal availability of surface water.

Materials and methods

Study Location

The *C. rugosa* population at Giddadella billabong, an ephemeral billabong located in central Arnhem Land, Northern Territory (134º21'S; 12º31.55'E), was studied over a 6 year period from 2000 to 2006 as part of a broad study focused on the demographic impact of *C. rugosa* harvesting in the Maningrida region. Giddadella is a traditional *C. rugosa* harvest site for the Rembarrnga people.

Radio-Telemetry

Towards the end of June 2005, turtles were caught at Giddadella over a two week period using fyke net traps. Forty turtles were chosen on the basis of size and sex. Carapace length was divided into eight size classes and five turtles were chosen at random from each size class (<130 mm, 130-145 mm, 145-160 mm, 160-175 mm, 175-190 mm, 190-205 mm, 205-220 mm, >220 mm). Where possible, turtles from both sexes were proportionately represented in each size class. Turtles were removed from the billabong for a period of seven days to secure Sirtrack® customized transmitters (Sitrack; Havelock North, New Zealand). Transmitter size was matched to body size to ensure that the weight of the transmitter did not exceed 7% of turtle weight (Schubauer, 1981). Transmitters were affixed by stainless steel bolts through holes drilled in the margin of the carapace (Tucker et al., 2001). Selly's Aqua Seal Putty® was used to create a level surface between the transmitter and the shell. In accordance with published protocols, the antenna trailed behind the turtle (Boarman et al., 1998). Transmitters were attached to turtles ranging in size from 111 – 276 mm. This allowed us to test the possibility that size influences turtle movement, timing and location of aestivation and survivorship.

After attaching the transmitter, turtles were held for a 5-6 day monitoring period before release. Turtles were released early July and tracking commenced after 7 days and continued until mid October 2005. As such, turtles were tracked prior to, during and immediately after the draw down period at Giddadella. Turtles were tracked at a standard three day interval using Telonics TR-4 receivers (Telonics; Mesa, AZ) fitted with Yagi collapsible antennas (model AY/C; Titley Electronics, Ballina, NSW). GPS location (Garmin 'GPS 72'; Garmin; Olathe, Kansas), water depth (to the nearest cm), and habitat were recorded for each animal on each tracking occasion. Turtle movement was calculated using the ArcView 3.2® extension Animal Movement Analysis (Hooge and Eichenlaub, 1997). Turtle location was successfully established on all occasions during the entirety of the study for 38 of the 40 turtles. Data from the two outstanding turtles were excluded from the analysis. Individual turtle movement was calculated as the distance between subsequent fixes according to the inter-tracking period. Average turtle movement was calculated as the average distance of movement between tracking events for non-aestivating turtles.

Radio telemetry was used to identify aestivation sites, and a probing stick (blunt 10 mm diameter steel rod) was used to confirm the precise location of the aestivating turtle. Location and description of the aestivation site was recorded, and four 250 mm steel pickets were used to construct a 1 m^2 plot around the aestivating turtle. Pickets were inserted into the ground to a depth of 100 mm. By minimizing picket height, and by spacing pickets 1 m apart, plot access by predators was not impeded. Since disturbance was monitored without entering the plot, there is no reason to believe that the construction of aestivation plots attracted predators. Every three days a digital photo was taken of the plot (Nikon D100®). Predator type was assessed by identifying tracks and scats within the plot. This procedure allowed us to identify the source and timing of predation within a three day period.

Aestivation depth relative to pig rooting depth was tested to determine whether *C. rugosa* avoid detection during aestivation by virtue of aestivation depth. Once Giddadella dried, a random selection of 100 pig roots (holes dug whilst feeding) was chosen according to published methodology (Hone, 1988). Mounded earth surrounding the root was removed and a steel rod was placed across the width of each root. A tape measure was used to measure root depth and straight-line vertical distance from the deepest point of the root to the steel rod.

Billabong Indices

Decrease in water surface area, water depth, invertebrate diversity and density, and increased water temperature were identified *a priori* as possible triggers of aestivation in *C. rugosa*. Water temperature was monitored hourly from early June – mid September using Hobo Water Temp Pro® data loggers (Onset Computer Corporation, Meadowbank, PA). Water temperature was measured at the deepest point of the billabong, at a depth of 10 cm from the bottom. Water surface area, water depth and standing invertebrate crop were recorded at fortnightly intervals. Surface area was calculated by circumnavigating the billabong recording location points at 100 m intervals using a GPS. ArcView GIS 3.2® software was used to calculate water surface area from perimeter location points. Surface area was scaled, by dividing observed surface area by maximum surface area recorded at the end of the wet season. Water depth was measured at a standard location with a tape measure. Standing invertebrate crop was measured according to published protocols (Georges et al., 1986) as follows. A column sampler (cross sectional area 0.07 m^2) was placed on the bottom at a water depth of 30 cm. All aquatic vegetation was removed from the column and placed into a sampling bucket. A small hand net (500 µm mesh) was moved 15 times through the water contained in the column and on each occasion the contents of the net were emptied into the sample bucket. Five replicates from each compass quarter (north, south, east and west) were taken on each sampling occasion. A basic sort of each sample occurred in the field, prior to being preserved in a 10% formalin solution. A secondary sort occurred prior to identification, counting and weighing. Where possible, invertebrates were identified to the family level.

Pig Gut Analysis

In the last week of July and the first week of August, 30 pigs were shot and dissected. The stomach, upper and lower intestines were removed for analysis. Pigs were shot by the Bawinanga Aboriginal Corporation Djelk Rangers in conjunction with the regional feral animal management plan for the Maningrida region. The pigs were shot at Damdam billabong, located approximately 80 km north east of Giddadella. Pigs were targeted as the billabong began to dry and turtles prepared for aestivation. Pigs were shot at first light whilst feeding in the billabong. Since pigs tend to harbour in the shade during the day (Bowman and McDonough, 1991), this sampling technique provided a high probability that each pig had spent at least part of the night feeding at Damdam billabong. Pigs with a body size greater than 50 kg were sampled. Males and females were sampled equally to prevent any possible sex bias in feeding location or food choice. Pigs were dissected on site. The stomach and intestines were bagged and transported back to laboratory facilities at Maningrida for analysis. The contents of the stomach and intestines were rinsed using a fine mesh sieve and spread across sorting benches. A presence / absence list was compiled for each sample. The proportional presence of each of the main dietary groups was estimated.

Harvest Rates of Turtles

Harvest rates at Giddadella were assessed between 2000 and 2006. Where possible, data were gathered by accompanying harvesters during harvest events. The straight-line carapace length and sex of harvested turtles were noted. This allowed us to test whether harvesters display a size / sex bias in harvesting. We were unable to accompany harvesters on all harvesting events. On these occasions, community members at Kolorbidahdah (location where the majority of harvesters reside) were asked to store the shells of harvested turtles. As such, our harvest estimates should be viewed as an index of harvest intensity. Although the community actively saved the shell of most turtles harvested from Giddadella, some turtles were sent to family members residing outside of Kolorbidahdah while dogs scavenged the shells of some other turtles. No attempt was made to include an estimate of shell loss in our harvest data and hence our harvest estimates rates display a degree of downward bias.

Statistical Analysis

The known fate extension of Program Mark 4.2 (Colorado State University; White and Burnham, 1999) was used to estimate survivorship during aestivation at Giddadella. The *R* statistical package v2.1.1 (*R* Development Core Team, 2005) was used for analysis external to Mark. Known fate models are the preferred method for testing survivorship using radio telemetry data (Heisey and Fuller, 1985; White and Garrot, 1990). Two turtles were eliminated from the data set because they did not meet the assumptions of the model; their fate could not be confirmed. A set of candidate models developed *a priori* was formulated in Mark and Akaike Information Criterion (AIC_c) corrected for small sample size was used as an objective means of model selection. The AIC_c chooses the most parsimonious model from a candidate set of models. This is the model with greatest support from the data (i.e. closest Kullback – Leibler distance to an unknown "truth"; Burnham and Anderson, 2001), given the bias corrected maximized log-likelihood of the fitted model and a penalty for the number of parameters used. Turtle size and days to aestivation were modelled as individual covariates. Average turtle movement of non-aestivating turtles and water surface area were averaged across all individuals in the population and modelled as across population covariates. The presence/absence of water was treated as a co-factor.

Taxonomic Clarification

Throughout this paper, our study species is referred to as the Northern Snake-necked Turtle *Chelodina rugosa* Ogilby, 1890. There is some confusion on this designation because the holotype of C. oblonga (Gray, 1841) is a specimen of our study species (Thomson, 2000). The name C. oblonga takes precedence. Strictly then, our study species is *C. oblonga*, a name that was applied to it up until 1967. Since then, it has been consistently but erroneously referred to as *C. rugosa*. However, an application is before the International Commission for Zoological Nomenclature (ICZN) to conserve current usage of the name *C. rugosa* Ogilby, 1890 for the Northern Snake-necked Turtle (Thomson, 2006). In the interests of stability of nomenclature, and because this application is under consideration by the ICZN, *C. rugosa* is used as the name of our study species.

Results

Location and Timing of Aestivation

Turtles generally aestivated amongst clumps or under fallen mats of the sedge *Eleocharis dulcis* (90%) rather than amongst the roots of paperbark trees *Melealuca leucadendra* (10%). Aestivation in *C. rugosa* did not occur at a specific, well defined point in time but rather turtles cumulatively entered aestivation over a 30 day period. Average turtle movement declined sharply prior to this period (Figure 4.1). Turtles entering into aestivation moved to the shallows (water depth < 12 cm) and partially buried themselves in the mud, digging deeper as the water receded. Once partially buried in the wet mud, turtles tended only to move in response to disturbance. Timing of aestivation was influenced by size, smaller turtles tending to aestivate earlier. Based on the evidence ratio (*ER*), the linear model was 22.31 times better supported by the data ([*w*[size] = 0.957] / [*w*[null] = 0.043] = 22.31). However, aestivation location (distance from aestivation site to the deepest point of the billabong) was independent of size. The null (intercept) model was 2.62 times better supported by the data.

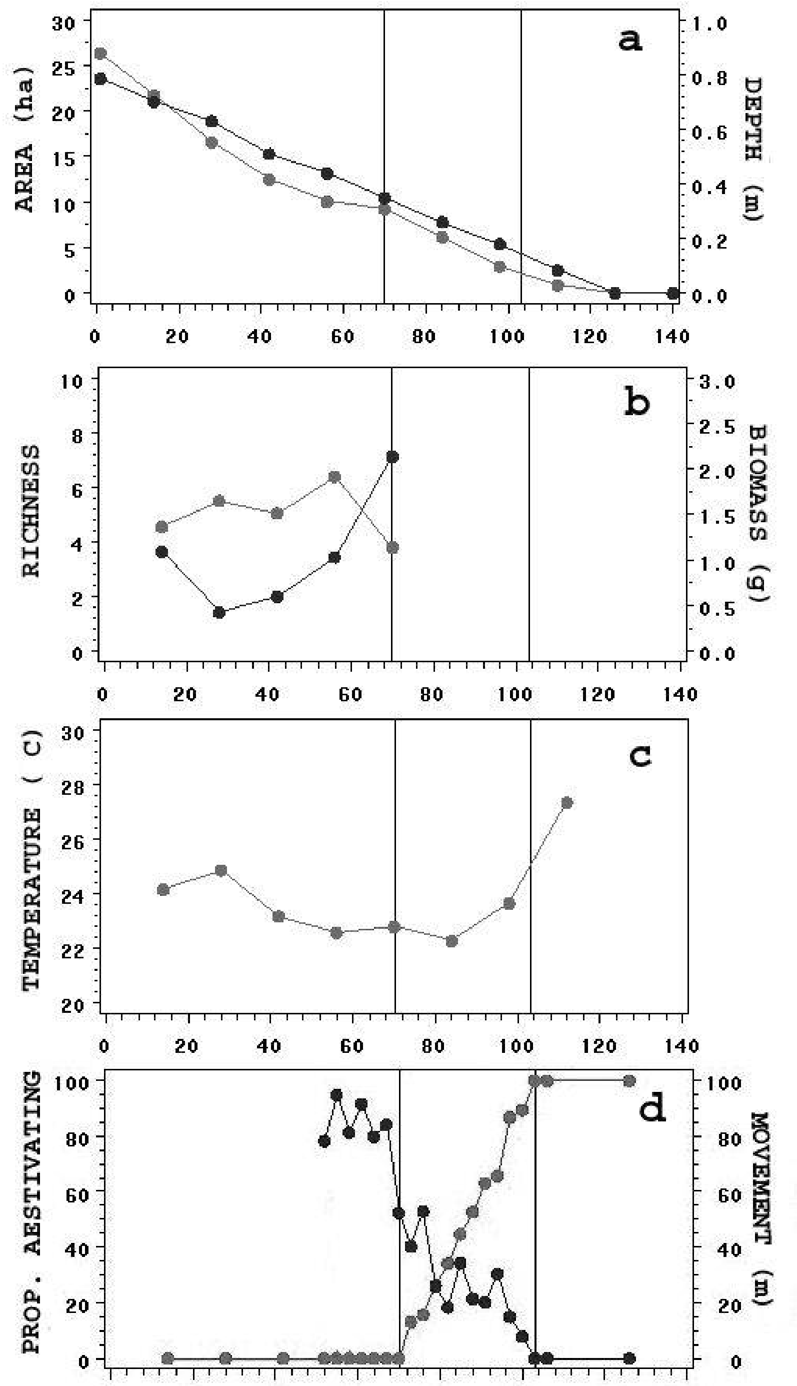


Figure 4.1: The draw down period at Giddadella is characterised by a linear decline in water surface area and water depth. Vertical bars characterise the window of opportunity available for initiating aestivation (**a**). Invertebrate biomass increased, while invertebrate diversity decreased prior to the final draw down period (**b**). Water temperature rose during this period (**c**). Turtles slowed their movement and entered into aestivation over a 30 day period (**d**). Cumulative count of aestivating turtles depicts aestivation as a gradual process, responding to one or a combination of factors such as a declining water area, declining water depth, declining invertebrate diversity and increasing water temperature. Note: the x-axis documents days from first monitoring period, not inter-aestivation period, see Methodology.

Water surface area and water depth declined prior to and during the final draw down period, while water temperature increased during this period (Figure 4.1). Invertebrate biomass increased immediately prior to the final draw down period, while invertebrate diversity declined. The observed increase in invertebrate biomass prior to the final draw down phase was the result of a high representation of singular species of backswimmer, family Notonectidae (Order: Hemiptera). The correlates tested failed to identify a single obvious cue for aestivation in *C. rugosa.*

Pig Predation

The fates of 38 of the 40 tracked turtles were successfully determined prior to, during and immediately after the final draw down period at Giddadella. The tracking history of the outstanding two animals was eliminated from the analysis since neither transmitter failure nor migration could be discounted. Of these 38 turtles, only 10 turtles (26%) were alive at the completion of tracking (Figure 4.2). Survival of unsexed juveniles (n = 5), males (n = 16) and females (n = 17) was low. Only 20% of juveniles, 19% of males and 35% of females were alive at the completion of the study. Furthermore, only 36% of turtles with carapace lengths equal to, or greater than, 165 mm (adult male and sub-adult and adult female turtles; Kennett 1994) survived. Pigs were the main predator. Recorded tracks and disturbance in aestivation plots indicate that pigs were the cause of 27 of 28 recorded deaths (96%). White Ibis (*Threskiornis molucca*) was identified as the only other predator of *C. rugosa*.

Pig dietary analysis confirmed that male and female pigs prey on *C. rugosa*. Shell fragments were found in the stomach and or large intestines of 16 of the 30 pigs sampled (53%) and of these 16 animals, 10 were male (62.5%) and 6 were female (37.5%). Vegetative bulbs and rhizomes of *E. dulcis* and *E. sphacelate* constituted the majority of each sample. Invertebrates, in particular red claw yabbies (*Cherax quadricarinatus*), were common. An estimate that 53% of pigs consumed turtle during the previous evening should be viewed as a minimum estimate because of the difficulty in identifying fragments of crushed turtle shell in pig dietary samples. Pigs do not tend to eat the shells of larger turtles and turtles consumed at the beginning of the evening may have passed through the

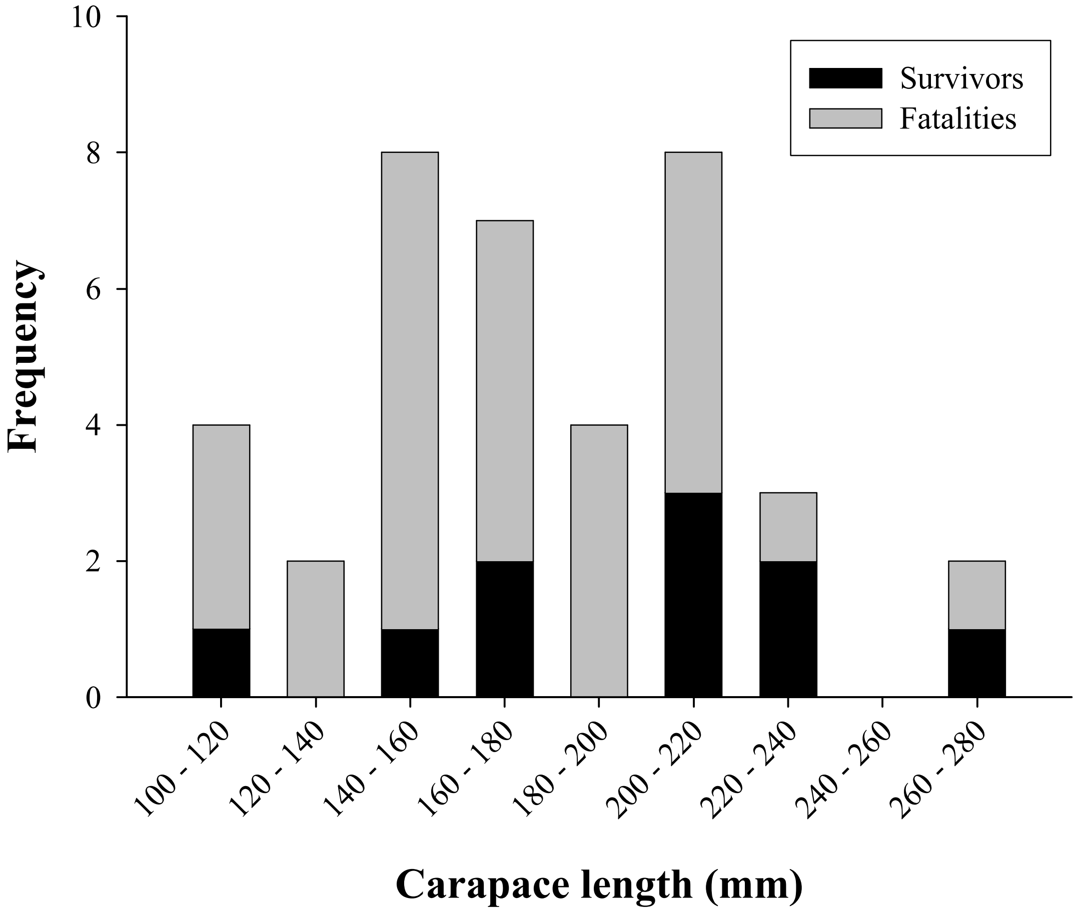


Figure 4.2: Survival of turtles tracked during the draw down period at Giddadella. Note that a large proportion of adult male and sub-adult and adult female turtles (carapace lengths equal to, or greater than 165 mm) died.

digestive system prior to sampling in the morning.

Pigs provide a steady predation pressure on *C. rugosa* during the final draw down period. Predation is alleviated only when the billabong dries and pigs disperse to the surrounding savannah (Figure 4.3). Photos of aestivation plots over time revealed that pigs target aestivating turtles. In 11 out of the 27 cases of pig predation (41%), pigs specifically located and dug up the aestivating turtle, leaving the remainder of the $1m^2$ plot undisturbed. This indicates that pigs actively seek out and prey on aestivating turtles. Shells of turtles with carapace lengths less than 160 mm tended to be heavily crushed during pig predation, the majority of the shell being consumed. In contrast, pigs favour the extremities (neck, leg and head) of larger turtles, leaving the shell damaged and only partially consumed. Aestivation depth did not exceed rooting depth and therefore did not assist *C. rugosa* survivorship. Average depth of aestivation was 11 cm ($n = 10$), while average rooting depth was 19.04 cm ($n = 100$). Aestivation depth was not influenced by body size. The null model was 6.8 times better supported by the data.

Aboriginal Harvest

Aboriginal harvest rates were extremely low at Giddadella. Harvests were attempted at the billabong in 2002 ($n = 13$), 2003 ($n = 10$), 2004 ($n = 8$) and 2005 ($n = 0$). Note that no turtles were captured during harvest events in 2005. The harvest regime focused on turtles with carapace lengths greater than 150 mm (Figure 4.4). As such, sub-adult and adult turtles were the harvested cohorts.

Survivorship Analysis

The most parsimonious survival model for *C. rugosa* at Giddadella over the study period was $\phi\ (m^+s^+w)$ ($AIC_c\ w = 0.8214$ out of a sum of 1.0); that is, survival (ϕ) was dependent on average turtle movement between tracking events, size, and the presence or absence of water at the billabong. A size-independent variant of this model $\phi\ (m^+w)$ received considerably less support from the data ($\Delta AIC_c = 4$; $AIC_c\ w = 0.111$) as did the model $\phi\ (m^+s^+a)$ ($\Delta AIC_c = 5.45$; $AIC_c\ w = 0.0539$), where water presence/absence was substituted with a measure of water surface area over time. All other candidate models lacked any

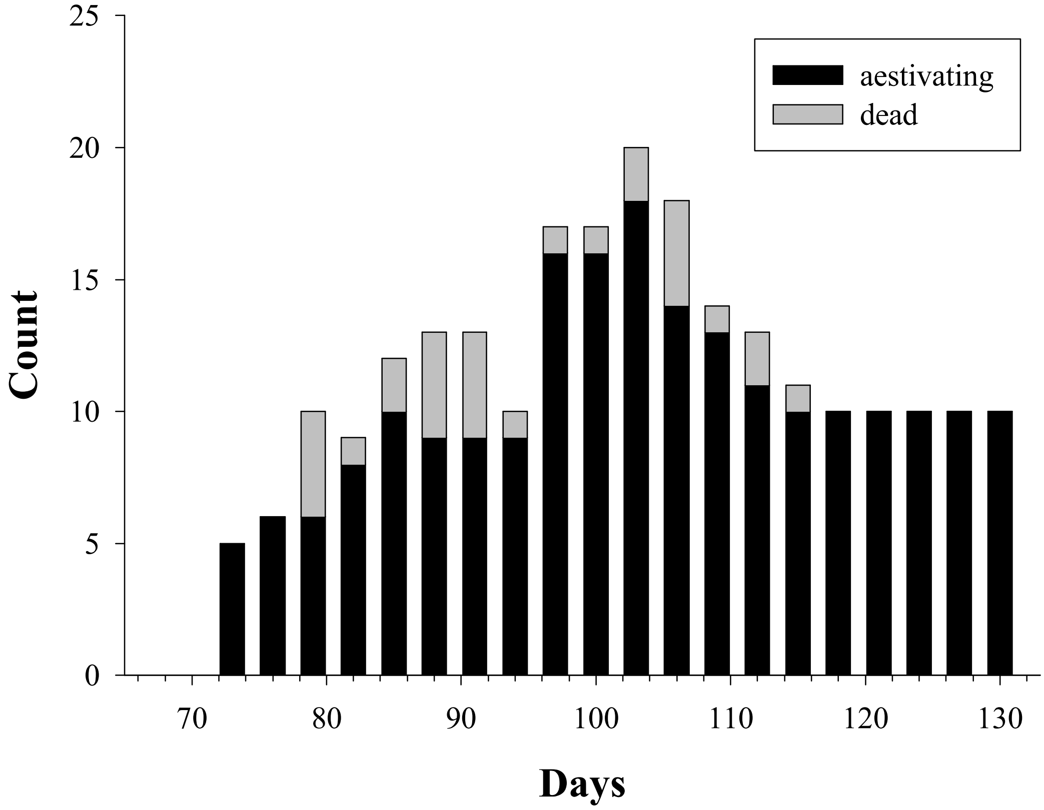


Figure 4.3: Predation of aestivating turtles during the draw down period at Giddadella. Note that turtle predation began shortly after turtles commenced aestivating (after 73 days of monitoring at Giddadella). Also note that predation ceased when the billabong dried (after 118 days of monitoring at Giddadella). Ten turtles were alive at the conclusion of the study.

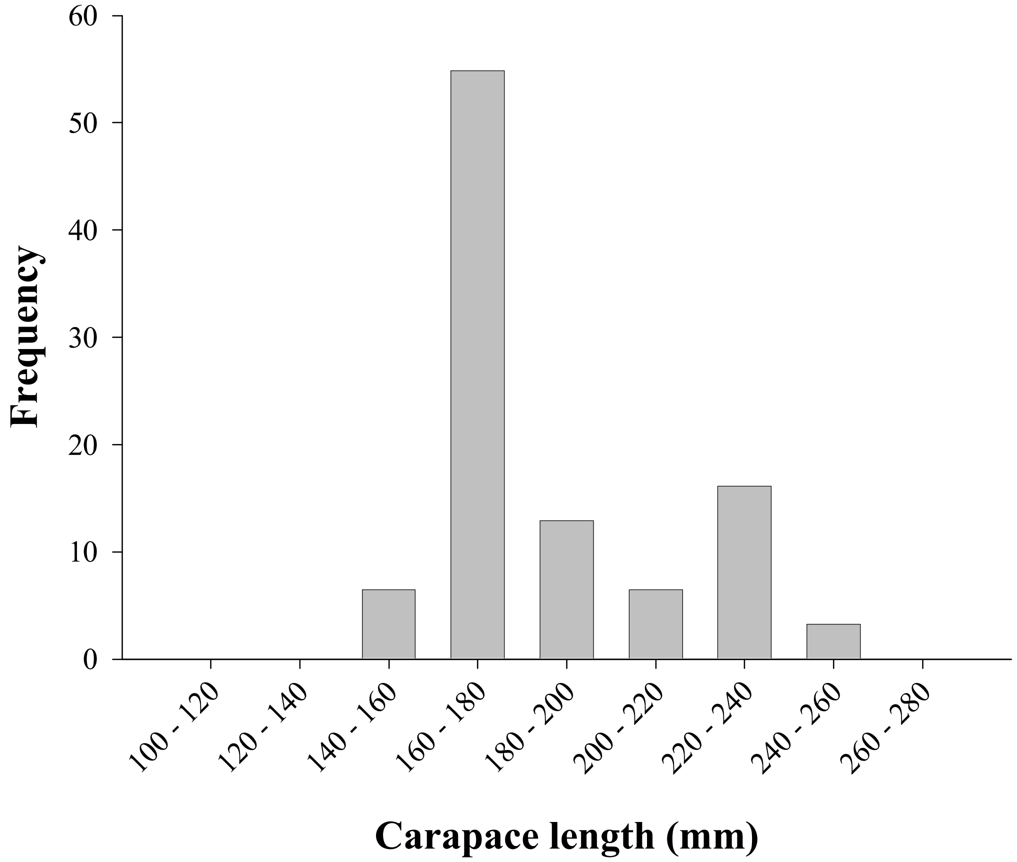


Figure 4.4: Turtles harvested at Giddadella from 2000-2005. Note that harvesting focused on turtles with a carapace length greater than 150 mm (adult and sub-adult turtles).

support from the data (Table 4.1). Note that the coefficients of the most parsimonious model (ϕ (m^+s^+w)) show that survival, although being positively influenced by size, decreases as turtles begin aestivating, returning to pre-aestivation levels once the billabong dried (Figure 4.5). Since decline in average turtle movement is a good proxy for initial aestivation (Figure 4.1), the importance of movement as a factor in the survivorship model demonstrates that early aestivation is a time of predator vulnerability. Survivorship of turtles over the tracking period of 81 days was $\phi = 0.2371$ (standard error = 0.0687) with upper and lower 95% confidence intervals of $\phi = 0.1286$ and $\phi = 0.3955$ respectively.

Discussion

Our radio-tracking monitoring demonstrates a number of remarkable results. First, survivorship *in C. rugosa* is greatly reduced during the end of the dry season when wetlands draw down and turtles aestivate. Only 26% of study animals tracked during the draw down period at Giddadella survived. Second, adult survivorship was heavily reduced during the draw down period. High adult survivorship in response to delayed maturity is often viewed as essential in achieving stability in turtle populations (Brooks et al., 1991b; Congdon et al., 1993, 1994; Heppell and Crowder, 1996; Hall et al., 1999). Turtles grow rapidly in size until maturity (a carapace length of 165 mm for male and 210mm for female *C. rugosa*; Kennett, 1994), maturing at a minimum size where survivorship remains high (Congdon and Gibbons, 1990; Gibbons and Lovich, 1990). Our results indicate that post-maturity size does not guarantee high survivorship in *C. rugosa*. Only 36% of turtles tracked with carapace lengths of 165 mm or greater survived the initial aestivation period. Third, the impact Aboriginal harvest rates have on *C. rugosa* survivorship is negligible compared to predation by feral pigs. Poor harvest success at Giddadella (traditionally a site of high harvest for Rembarrnga people) appears to be the direct result of harvesters competing with pigs for a seasonal food source.

Aestivation in *C. rugosa* does not occur at a specific, well defined point in time, but rather over the weeks prior to the billabong drying. Turtles move to the shallows and partially bury themselves in the mud, digging deeper as the water recedes and moving only in response to disturbance. Turtles at Giddadella did not emerge from the billabong to

Table 4.1: Complete survivorship model set showing Akaike's Information Criterion (AIC_c), number of parameters, deviance, and model weights. Model names reflect parameters used in the model. Turtle size (*s*), days to aestivation (*da*), average movement between tracking events (*m*) and water surface area (*a*) were modelled as covariates. Water presence / absence (*w*) was treated as a co-factor (refer to methods). The time constant model (.) was also modelled.

Model	AIC_c	Parameters	Deviance	Delta AIC_c	Weight
$\phi\ (m^+ s^+ w)$	186.733	4	180.698	0	0.828
$\phi\ (m^+ w)$	190.736	3	186.719	4	0.112
$\phi\ (m^+ s^+ a)$	192.183	4	184.124	5.45	0.054
$\phi\ (m^+ s)$	196.847	3	190.812	10.11	0.005
$\phi\ (m)$	200.84	2	196.822	14.11	0.001
$\phi\ (a)$	216.017	2	211.999	29.28	0
$\phi\ (w)$	228.492	2	224.474	41.76	0
$\phi\ (s)$	229.615	2	225.598	42.88	0
$\phi\ (.)$	229.782	1	227.776	43.05	0
$\phi\ (da)$	231.773	2	227.756	45.04	0

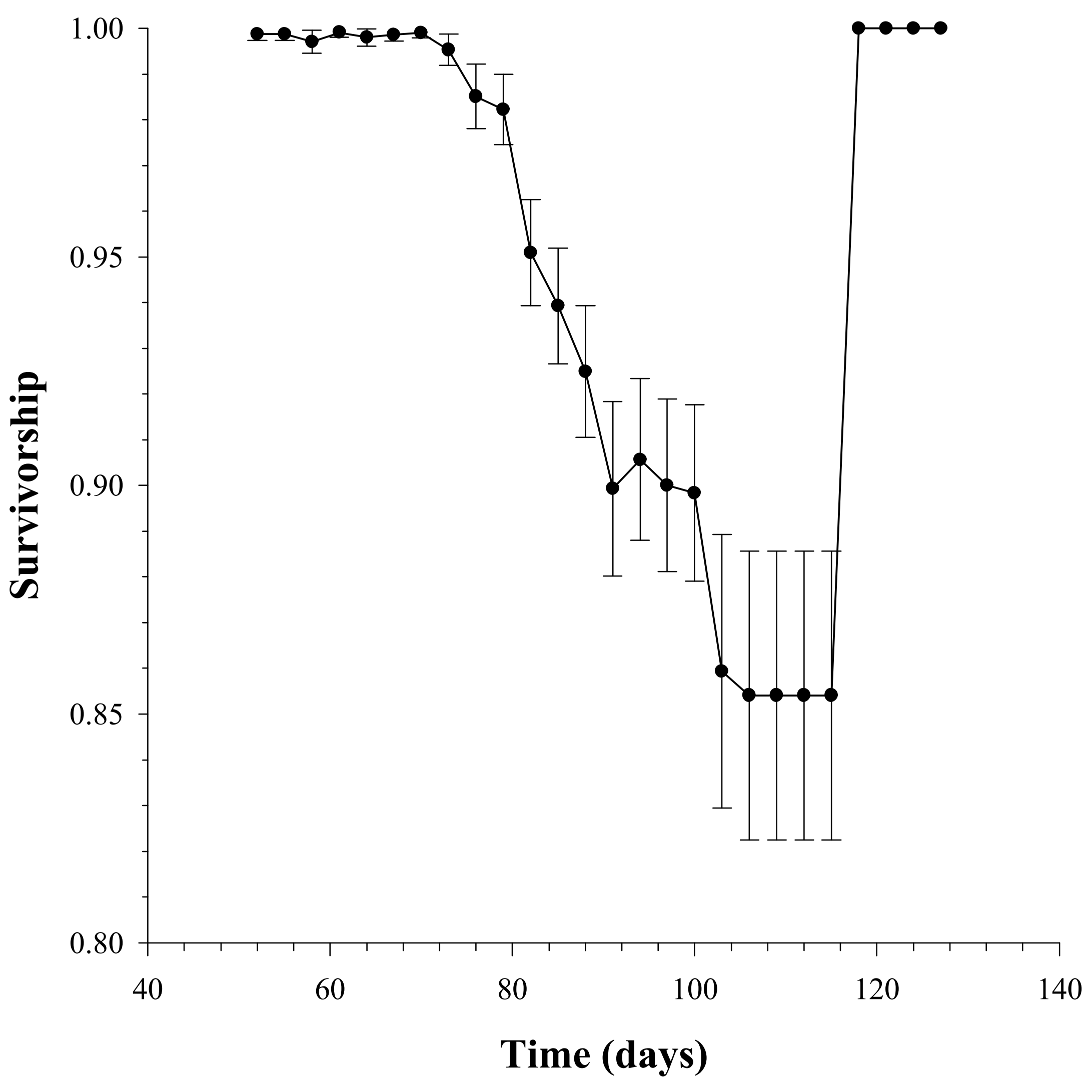


Figure 4.5: Survivorship at Giddadella according to the most parsimonious model ϕ $(s^{+}m^{+}w)$. Note that survivorship levels begin to drop once turtles start to enter into aestivation (after 73 days) remaining relatively low until the billabong dries (after 118 days).

aestivate in a dry substrate, as has been previously suggested for *C. rugosa* (Grigg et al., 1986). Turtles that commence aestivation in the shallows breathe by raising their head above the water surface (Kennett and Christian, 1994). In turn, breathing constrains turtles from initially burying themselves deep in the mud. Aestivation in *C. rugosa* is probably an adaptive response to a number of interacting factors during the final draw down period, such as declining water availability, increased water temperature and decreased invertebrate diversity (Figure 4.1).

Survival rates recorded for *C. rugosa* at Giddadella are much lower than previous estimates for this species (Kennett, 1994) and for turtles in general (Frazer et al., 1991; Iverson, 1991; Congdon et al., 1993; Spencer and Thompson, 2005). We are confident that the tracking procedures used in this experiment did not bias our survivorship estimate in a downward direction. Human interaction between tracker and turtle was minimized at all times. Transmitter weight did not exceed 7% of turtle body mass and hence did not restrict turtle movement (Schubauer, 1981). Rather, low *C. rugosa* survival at Giddadella is a direct response to high pig abundance during the final draw down period. Feral animal numbers were relatively low and harvesting absent at previously studied populations and, in turn, *C. rugosa* survivorship was measured to be relatively high (Kennett, 1994). Survivorship of *C. rugosa* at Giddadella, according to the most parsimonious survivorship model $\phi\ (s^{+}m^{+}w)$, reveals that size positively promotes survival during the final draw down phase, when turtles commence aestivation, burying in the mud and ceasing daily movement and thus minimising daily expenditure (approximately 30 days at Giddadella in 2005). During this period the billabong had drawn down, but had not dried completely. Pigs concentrate around available water during the late dry season in northern Australia (Caley, 1993; Twigg et al., 2005). Accordingly, pigs dispersed from Giddadella when the billabong dried, causing survival rates to return to a level similar to that observed prior to the final draw down phase (Figure 4.5). The challenge is to interpret these new findings in context, where aestivation is not necessarily an annual event, where rock paintings and ceremonial stories indicate that turtle populations have survived an antiquity of many millennia of harvesting (Chaloupka, 1993) and where recently invasive pigs are now in high abundance across northern Australia (Caley, 1993; Corbett, 1995).

Harvest methods used to gather *C. rugosa* today differ little from those used historically (steel rods are often substituted for wooden digging sticks) and as such the contemporary harvest regime can be viewed as a window to the past. Harvesters still use the excavation mound and the breathing hole of aestivating turtles as the primary method for locating *C. rugosa*. The data presented in this paper show that harvesting focuses on sub-adult and adult turtles (Figure 4.4), the most important cohort for achieving population stability (Crouse et al., 1987; Heppell and Crowder, 1996; Heppell, 1998). *C. rugosa* grows quickly, matures at a young age and is highly fecund (Kennett 1996, 1999). Such demographic characteristics promote population stability in environments where adult survivorship is low (Fitzgerald, 1994; Shine et al., 1996; Webb et al., 2002). Although our data suggest that contemporary harvest rates of *C. rugosa* in Arnhem Land are minimal, as recently as 10-20 years ago *C. rugosa* provided an important seasonal source of protein for Aboriginal people in Arnhem Land (Altman, 1984; White and Meehan, 1993; Russell-Smith et al., 1997). Our data suggest that the observed decline in harvest rates do not reflect over harvesting, or a cultural shift in the emphasis placed on turtle harvesting today, but rather declining harvest rates are the direct result of the timing and severity of *C. rugosa* pig predation. The harvest techniques used to gather *C. rugosa* limit harvesting to a dry environment. Since pig predation causes a substantial decline in *C. rugosa* survival rates during the weeks prior to drying, pigs deplete harvest stocks immediately before the harvest event, in turn causing harvest success to decline. Harvest rates are further compromised by pigs rooting billabongs whilst digging up the bulbs and roots of *E. dulcis*, *E. sphacelate* and *Nymphaea sp.*, making the location of aestivating turtles a difficult task.

Our research spawns an interesting question. Do pigs prey upon a proportion of the turtle population that would otherwise be doomed as a result of customary harvesting? Evidence suggests that *C. rugosa* achieve relatively high survivorship rates in the absence of high pig densities (Kennett, 1994). As such, it is logical to assume that this would in turn convert to increased harvest efficiency, especially since harvest efficiency rises when feral animals are absent or in low density during the draw down period (Fordham, unpublished data). Therefore, it is probable that harvesting would have otherwise sealed the fate of a proportion of the turtles predated by pigs at Giddadella. However, the potential threat pigs pose to *C. rugosa* populations in Arnhem Land is not necessarily lessened by the fact that pig predation, to an extent, replaces Aboriginal harvesting.

Persistence of *C. rugosa* in Arnhem Land historically has been influenced by a combination of stochastic rainfall and cultural practices on customary harvest rates. Although billabongs annually rise and fall in accordance with the monsoonal wet season and the intervening dry season, draw down and billabong drying is not necessarily an annual event. Rainfall in northern Australia is subject to extreme temporal variation (Taylor and Tulloch, 1985; Georges et al., 2003), providing years where *C. rugosa* aestivate and years where aestivation is not required. In years where aestivation is not required, survivorship remains high and the compensatory mortality period is extended; these are boom years (2000 and 2001 at Giddadella). Conversely, in dry years billabongs draw down, the turtles aestivate and survivorship is low; these are potentially the bust years (2002-2005 at Giddadella). However, Aboriginal people are bound by cultural responsibilities that are reinforced through participation in ceremonies and rituals (Berndt and Berndt, 1970). These cultural practices often mean that billabongs are left unharvested since ceremonies in Arnhem Land often coincide with the late dry season when *C. rugosa* are harvested. Furthermore, traditional estates are often periodically closed for ritual purposes, meaning subsistence hunting and gathering is prohibited creating spatial refugia (Fordham, unpublished data). Before the introduction of pigs, these potential bust years would have constituted boom years for those local *C. rugosa* populations. The frequency of boom years, seasonally driven as well as by lapses in Aboriginal harvest, matched with a favourable set of life history traits, have enabled *C. rugosa* populations in Arnhem Land to withstand a history of adult harvesting. The arrival of pigs, with their unrelenting attention to turtle predation, has changed this dynamic. The high rainfall boom years for turtle survivorship, no longer complemented by years in which Aboriginal harvest is interrupted by cultural activity, are now likely to be much more important in determining adult survivorship and the stability of populations of *C. rugosa* in Arnhem Land than before pigs arrived.

A comparison of pig predation on *C. rugosa* with fox (*Vulpes vulpes*) predation on the Murray turtle (*Emydura maquarii*) illustrates the importance of boom years and favourable life history traits to the persistence of *C. rugosa* in Arnhem Land. Foxes, an animal exotic to Australia, prey on nesting *E. maquarii* (Thompson, 1983; Spencer, 2002). Although survivorship rates of *E. maquarii* are relatively high compared to those recorded for *C. rugosa* at Giddadella, fox predation may cause long-term population decline in *E. maquarii*, primarily because the life history traits of *E. maquarii* are ill-equipped to compensate quickly for adult predation during the interbreeding season and, in the absence of human intervention, predation is an annual event (Spencer and Thompson, 2005).

The direct conservation implications of pig predation on *C. rugosa* in Northern Australia remain uncertain. The present study shows that *C. rugosa* populations can potentially persist despite episodes of heavy pig predation if wet years are frequent, providing annual persistence of water at seasonal billabongs, since survival rates remain high in the absence of drying. The harvest and related cultural implications of pig predation are clearer. Dietary studies of Aboriginal people in central Arnhem Land indicate that pigs were locally rare or nonexistent only 30 years ago (Altman, 1984, 1987), and as such it is likely that pig populations in Arnhem Land are yet to reach carrying capacity. Since pigs are the main predator of *C. rugosa*, one can expect that *C. rugosa* survivorship will decline further with increased pig abundance and, in turn, *C. rugosa* harvest efficiency in Arnhem Land will continue to dwindle. In the near future Aboriginal people may have no choice but to abandon the harvest of *C. rugosa*, an action that will have damaging cultural consequences. The cultural reinforcements linked to harvesting and preparing traditional foods exceed dietary requirements associated with forging a subsistent lifestyle (Collins et al., 1996; Freeman, 1997). Harvesting provides an important conduit for the generational transfer of traditional knowledge and cultural history. The forced abandonment of *C. rugosa* harvesting in response to predation by feral pigs threatens to constitute yet another hardship on indigenous societies in northern Australia. Customary harvest rates are already compromised by the invasive cane toad (*Bufo marinus*; Altman et al., 2003), an exotic anuran that threatens the persistence of a number of terrestrial reptiles in northern Australia (Burnett, 1997; Phillips et al., 2003). However, pigs in Arnhem Land present a management paradox since feral animals often constitute a culturally and economically important resource for indigenous people (Altman, 1982; Bowman and Robinson, 2002). Communities at a regional level must collectively choose between an annually available food source in the form of pig meat and conserving the traditional harvest of *C. rugosa*, a food source that is at best seasonally abundant. Effective management can only be achieved if all stakeholders choose to view pigs as a pest (Robinson and Whitehead, 2003). Management issues that are a direct legacy of post colonialism, such as formerly domesticated feral animals, often rely upon the amalgamation of traditional and western scientific practices to achieve "healthy" country (Barker et al., 2001; Whitehead et al., 2003). Accordingly, it is imperative that government agencies and scientists work together with indigenous communities to outline both the potential threat pigs pose to harvest rates and possibly the persistence of *C. rugosa*, and the management options available to manage pig abundance in Arnhem Land such that *C. rugosa* harvesting can continue into the future as it has for countless generations.

Predictive demographic models that incorporate stochastic rainfall, recruitment, pig densities and any compensatory responses to predation are urgently required to assess the population dynamics and persistence probabilities of *C. rugosa* in Arnhem Land. In doing so, this research will provide further insight into the conservation threat pigs pose to *C. rugosa* populations across Northern Australia.

Density dependent responses to indigenous harvesting and predation of snake-necked turtles in tropical northern Australia.

Picture: Christene Campion [M. Hatt]

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Summary

Many chelonians have low hatchling survival, slow growth, delayed sexual maturity and high sub-adult and adult survival, constraining their ability to respond quickly to an increase in adult mortality from direct impacts such as harvesting or indirect impacts such as from habitat alteration. By contrast, *C. rugosa* is fast growing, early maturing and highly fecund relative to other turtles. Here we provide correlative evidence spanning six study sites and three field seasons, which indicates that *C. rugosa* can persist under conditions of relatively low sub-adult and adult survival caused by pig predation and customary harvesting by people. Compensation is achieved via density dependent adjustment of life history parameters. A decline in density caused by low adult and sub-adult survival due to harvest and predation was correlated with an increase in recruitment and age-specific fecundity, via enhanced juvenile survival, decreased size at onset of maturity, and increased post maturity growth. These findings challenge the generality that high sub-adult and adult survival is crucial for achieving long-term population stability in long-lived vertebrates, such as chelonians. We instead posit that long-lived species with 'fast' recruitment, similar to *C. rugosa*, are able to persist in the face of occasional or sustained adult harvest without necessarily threatening population viability, thanks to a strong compensatory density dependent response.

Introduction

Density dependent processes appear to regulate the abundance of a wide range of organisms (Brook & Bradshaw 2006). Such processes compensate for sporadic reductions in density, providing resilience by assisting population recovery after downward displacement of population numbers (Sinclair & Pech 1996), even in long-lived reptiles such as *Crocodylus porosus* (saltwater crocodile; Bradshaw *et al.* 2006). The same compensatory processes that provide resilience to perturbation also afford resistance to chronic depression of abundance. For example, downward pressure on bird abundance by harvest can be resisted by dynamic adjustment of survival or fecundity (Nichols *et al.* 1984). Similarly, compensatory mechanisms are thought to enhance persistence of some reptile populations during periods of reduced survival (Massot *et al.* 1992), but there have been few comprehensive studies explicitly addressing these demographic issues in chelonians. Studies to date (Stubbs *et al.* 1985; Brooks, Brown & Galbraith 1991b; Bjorndal, Bolten & Chaloupka 2000; Tiwari *et al.* 2006) have been limited by: (i) lack of appropriate replication; (ii) focus on a compensatory shift in a single demographic parameter (such as juvenile growth and its interaction with age of maturity) rather than an assessment of all potential compensatory responses; and (iii) the use of indirect evidence of differential survival probabilities such as levels of habitat disturbance rather than direct measures of survival.

Life history traits of long-lived vertebrates constrain the ability of populations to respond to chronic increases in mortality (Heppell, Caswell & Crowder 2000) because compensatory responses are limited and recovery is slow (Musick *et al.* 2000). Among amniotes, turtles characteristically have a life history strategy of high fecundity accompanied by low egg and hatchling survival, slow growth, late maturity and high juvenile and adult survival (Heppell 1998; Chaloupka & Limpus 2002). Thus turtles are typically viewed as having ‘slow’ life histories, and as such, harvesting the small fraction of individuals that survive the vulnerable early life history stages may jeopardise population persistence, because these individuals have high reproductive potential (Cunnington and Brooks 1996; Heppell *et al.* 1996). However, a universal perception on freshwater turtle vulnerability to harvest, based on deterministic models (Congdon, Dunham & van Loben Sels 1993, 1994), should be interpreted with considerable care (Mills, Doak & Wisdom 1999). A ‘slow-fast’ continuum in life histories exits for a range of taxa, including mammals (Heppell *et al.* 2000), birds (Saether, Ringsby & Røskaft 1996), reptiles (Webb, Brook & Shine 2002) and sharks (Smith, Au and Show 1998), and a species position along this continuum influences how population growth will respond to change in a demographic trait (Saether & Bakke 2000). It may be that high rates of survival are crucial for some turtle species (Brooks *et al.* 1991b; Chaloupka 2002), while the life history traits and population dynamics of other species may better equip them to compensate some level of increased mortality through predation or harvest, as is the case with condrichthyans (Stevens *et al.* 2000).

Traits that contribute heavily to population growth in long-lived vertebrates, such as adult survival, tend to be buffered against changes in population density or stochastic factors (Pfister 1998). Alternatively, traits such as juvenile survival and somatic growth contribute, proportionately less to population growth, but are more sensitive to variation (Fowler 1987; Gaillard, Festa-Bianchet & Yoccoz 1998). Today, as in the past, wild populations of sub-adult and adult turtles are commonly harvested for both subsistence and commercial purposes (Gibbons *et al.* 2000; Georges, Guarino & Bito 2006a). Some marine turtle populations may compensate for decreased abundance by adjusting life history parameters, such as somatic growth or fecundity, as a response to reduced density (Bjorndal *et al.* 2000; Tiwari *et al.* 2006), but the prevailing perception is that freshwater turtles do not display a density dependent response in reproductive effort, recruitment or somatic growth (Brooks *et al.* 1991b). According to this view, fixed demographic parameters constrain the ability of freshwater turtle populations to recover following population depression and limit their ability to respond to a chronic increase in adult mortality, whether it be direct through harvesting, or indirect through habitat alteration (Converse, Iverson & Savaidge 2005). Thus the harvest of adult turtles at almost any level is often regarded as inherently unsustainable, and therefore unacceptable (Congdon *et al.* 1993, 1994).

The issue of the resilience of response to harvest is particularly relevant to the northern snake-necked turtle *Chelodina rugosa* (Ogilby 1890). It is a fast growing, early maturing and highly fecund species in comparison with many other turtles (Kennett 1996, 1999). It attains high densities in the ephemeral swamps and other wetlands of the wet-dry tropics of northern Australia. Turtle activity is punctuated each year by the dry season, when the wetlands draw down and often completely dry. Immediately before drying, turtles move to the shallows, bury in the mud and aestivate (Kennett and Christian 1994). Historically, aestivating *C. rugosa* provided a source of protein for indigenous communities living on, or near, ephemeral wetlands (Russel-Smith *et al.* 1997). Today, harvest rates by people are negligible primarily because pigs (*Sus scrofa*; Linnaeus 1758), an exotic predator, deplete stocks immediately before harvesting is possible (Fordham *et al.* 2006b). Rainfall in the wet-dry tropics is highly variable, both within and across years, in the quantity that falls and its timing (Taylor and Tulloch 1985). In unusually wet years billabongs (large waterholes) do not dry, turtles do not aestivate, and thus harvesting and pig predation is limited. These refugial years are potentially important for local population persistence of *C. rugosa* (Fordham *et al.* 2006b).

Here we evaluate whether long-term population persistence, in the face of chronic low adult and sub-adult survival caused by pig predation and Aboriginal harvesting, is made possible by compensatory demographic responses in *Chelodina rugosa*, a turtle species with relatively 'fast' life history traits.

Materials and methods

Study Location and Experimental Design

Six discrete populations of *C. rugosa* were studied in central Arnhem Land, Northern Territory, Australia, from 2002 until 2006. Billabongs were selected to be representative of the variation in frequency of drying and frequency of harvest. Two of the six populations, Giddadella (12º31.55'S; 134º21'E) and Damdam (12º10'S; 134º37.5'E) dried annually, and were subject to harvesting at least once per year during the period of study (except in 2004, when Damdam was closed to harvesters for ritual purposes). A further two populations, Murrybulljuluk (12º37'S; 134º50.9'E) and Little-Giddadella (12º30.7'S; 134º21.6'E) dried annually, but were rarely harvested because of their relative isolation or historical pattern of use. Little-Giddadella had no record of harvest. Murrybulljuluk was harvested in 2003, an event that had not occurred for at least 15 years prior (Otto Bulmaniya Campion, personal communications). The remaining two populations, Imimbar (12º44'S; 134º31.8'E) and Ginmilly (12º19.1'S; 134º30.05'E) typically do not dry in any year and therefore are unharvested. Pig predation was not controlled as part of the experimental design as the influence of pigs was not appreciated until the work was underway. Level of pig predation was incorporated as an uncontrolled covariate. These six populations were used to compare key demographic parameters, such as survival, juvenile recruitment, growth, fecundity and size of maturity and to determine their correlation with billabong permanence, harvest regime and feral pig abundance. The interaction between survival, harvest and pigs was calculated using the entire data set (2002 – 2006), while all other demographic traits were calculated using data collected only in 2003 and 2004. This was necessary because only the dry seasons of 2002 and 2003 offered environmental conditions suitable to the experimental design. All six populations were located at least 1.5km from the nearest water body. *C. rugosa* do not migrate when discrete waterholes dry (Fordham *et al.* 2006b), though a low level of dispersal occurs during rare flooding events (Fordham unpublished data). As such, the location of each population ensured that emigration and immigration were sufficiently low so as not to invalidate our demographic analysis.

Trapping and Measurement Procedures

Each population was trapped twice per year from 2002 to 2005. In 2005, Damdam and Murrybulljuluk dried earlier than usual which restricted trapping while in 2006, turtles were caught only once at the end of the wet season. The methodology used to capture and mark turtles; measure turtle size and weight; sex and age turtles; estimate size of maturity, female reproductive activity and clutch frequency; determine clutch size relative to body size; and to class turtles as either hatchlings, juveniles, sub-adults or adults, is described in detail in Appendix 5.1.

The *R* statistical package v2.1.1 (*R* Development Core Team 2005) was used to assess the statistical relationships between population variation in gravid turtle size, clutch size and post maturity growth. Bootstrapping, where data were repeatedly sampled with replacement (1,000 – 10,000 times), was used to estimate the standard error and confidence intervals via the percentile method (Crawley 2002). Generalised linear models were used to test whether clutch size or mass varied among populations or covaried with survival rate.

Modelling Growth

Growth rates were estimated from annual capture data (captures before drying or at the end of the dry season: September to October). Growth rate was calculated as the incremental difference in carapace length divided by the number of years between captures. Von Bertalanffy, Gompertz and logistic curves were fitted to growth data separately for male and female turtles at each population, using published protocols (Frazer, Whitfield

Gibbons & Greene 1990) implemented in PROC NLIN in SAS Version 8 (SAS Institute 2001). Although nonparametric approaches have been advocated for sea turtles (Chaloupka and Musick 1997; Bjorndal *et al.* 2000), the simple parametric approach employed in this study has provided good estimates of the age-size relationship in *C. rugosa* (Kennett 1996) and other congeneric species (Spencer 2002; Spencer, Janzen & Thompson 2006). The von Bertalanffy model had the smallest residual mean square (degrees of freedom equal across models) and hence was the model subsequently used. The age-size relationship was calculated using the equation:

$$Age = \frac{\ln[1-(h/a)] - \ln[-(Lr/a)+1]}{k} \text{ .... (1)}$$

where, h = CL at hatching (mm), a = asymptotic CL (mm), Lr = CL (mm) and k = growth parameter. Size at hatching equaled mean *C. rugosa* hatching size (carapace length = 33.28 mm, n = 135; Fordham unpublished data). Bootstrapping was used to estimate the standard error and 95% confidence limits for age.

Aboriginal Harvest

Harvest data were typically collected directly during harvest events. When we were unable to accompany harvesters, community members at Kolorbidahdah, Damdam and Wurdeja outstations (settlements where the majority of harvesters reside) were asked to store the shells of turtles harvested at Giddadella and Damdam, leading to unmeasured underestimation in the true harvest rate (Fordham *et al.* 2006b). Communities in the near vicinity of the two seasonal, but rarely harvested billabongs, were contacted regularly during the harvest season to determine whether harvesters had visited these billabongs. The size and sex of harvested turtles was also recorded, when possible, to assess whether Aboriginal people display a size or sex bias in turtles that are selected for harvest.

Pig Rooting and Abundance

Pig rooting (soil disturbance caused by digging for food items) was used as an indicator of pig abundance (Hone 1988). Pigs congregate at billabongs as they draw down, dispersing shortly after the billabong dries (Fordham *et al.* 2006b). Thus, pig rooting was only measured at billabongs that annually draw down and dry, estimated from data collected 2-4 weeks after drying. Transects were established for each compass quarter (north, south, east and west), by laying a tape from the centre of the billabong (site of the last remaining water) to the maximum perimeter. Pig rooting was estimated as a percentage disturbance directly under the tape for each alternate 10 m interval. Pig rooting was classed as severe if percentage rooted exceeded 20% and minimal if less than 20%.

Modelling Survival

Program Mark 4.2 (Colorado State University; White and Burnham 1999) was used to estimate *C. rugosa* survival (ϕ) and recapture rates (p). The joint analysis of live and dead encounters of marked animals as described by Burnham (1993), which include an estimate of recovery rates (r) and site fidelity (f), was used to estimate ϕ and p at regularly drying billabongs. Data on turtle mortalities were obtained by regularly circumnavigating all billabongs before and during drying, by accompanying harvesters on harvest activities and by surveying communities that lie within a close proximity of harvested billabongs. Recovery rates met the assumption of the Burnham model; there was no substantive bias in the recovery of dead turtles from different mortality sources (Francis and Cooke 1993). Site fidelity was fixed to 1 (100 %), because (i) emigration and immigration were minimal owing to choice of study site (discrete, distant billabongs) and (ii) *C. rugosa* tend to aestivate rather than move in response to the periodic absence of water (Fordham *et al.* 2006b). The standard Cormack-Jolly-Seber recaptures only method was used to model survival at rarely drying billabongs because dead recoveries were rare or non-existent.

Two candidate model sets were formulated in Program Mark before analysis; one for seasonal billabongs, and another for rarely drying billabongs. Akaike's Information Criterion, corrected for small sample size (AIC_c), was used as an objective means of model selection (Burnham and Anderson 2001). Turtle CL was modelled as an individual covariate. Turtles with carapace lengths < 140 mm (juveniles) and $\geq$ 140 mm (adult males and sub-adult and adult females), were considered grouped factors (levels). Where trapping period varied from the standard 20 day period, a relative index of trapping period, averaged across all individuals in the population, was modelled as an across-population covariate. In addition, the presence or absence of water, harvest and the monsoonal rains were treated as co-factors, as was the severity of pig rooting.

The candidate model set was used to test whether periodic absence of water, pig abundance and harvest determine turtle survival and recapture probabilities and whether size is an important covariate. We hypothesized (*a priori*) that survival would decline markedly in response to harvest and pig abundance and that size would positively influence survival in populations where negative perturbations in abundance are rare. Survival and recapture probabilities were model-averaged using Akaike Weights (w_i) to include model uncertainty in the estimates of parameter precision (Buckland, Burnham & Augustin 1997). The importance of individual covariates in the models constrained the available goodness-of-fit tests (Telfer *et al.* 2002). Goodness-of-fit was evaluated by comparing the deviance of the explanatory models with reference to the deviance of the null model. In each case the saturated model explained greater than 74% of the deviance, and thus, adequate model fit was concluded. Recapture probabilities were used to calculate population abundance using the Horvitz-Thompson type estimator {$N_i = (n_i/p_i)$; Seber 1982}, where n_i is the number of turtles captured, p_i is the recapture probability and N_i is population abundance in the *i*th year. Approximate 95% confidence intervals were derived from the model-averaged standard error of p_i based on a normal approximation.

Results

Aboriginal Harvest

Aboriginal harvests were attempted at Giddadella in 2002 (number taken [*n*] = 13 turtles), 2003 (*n* = 10), 2004 (*n* = 8) and 2005 (*n* = 0) and at Damdam in 2002 (*n* = 38), 2003 (*n* = 14) and 2005 (*n* = 0) and Murrybulljuluk in 2003 (*n* = 38). Note that harvesters did not capture any turtles in 2005 at either of the two seasonal, regularly harvested billabongs, despite attempting harvests. The size distribution of harvested turtles included only adult and sub adults (carapace length >140 mm; Appendix Figure 5.4).

Survival Analysis

Annually Dry, Harvested, Pig-impacted Billabongs: According to the most parsimonious survival model for Giddadella, severity of pig rooting had the largest influence on survival (ϕ) and recapture rates (p), while recovery rates (r) were influenced by the presence or absence of water and turtle size (Table 5.1; see Appendix Table 5.4 for entire model set). A second acceptable model, ranked lower, but not substantially so, modelled ϕ and p as a factor of turtle size as well as severity of pig rooting (Table 5.1). There was weaker support for the next ranked model, which had ϕ and p driven by water presence or absence rather than pig rooting (Table 5.1). Turtle harvesting was attempted at least once during each drying period, and as such, harvest could not be disentangled from drying *per se*. In any case, the relative lack of support for this third model indicates that severity of rooting has a greater influence over ϕ and p at Giddadella than harvest. Model-averaged survival probabilities (weighted by AIC_c support) were relatively high [$\phi = 0.708$; 95% confidence intervals (CI) = 0.591–0.802] when rooting was low or absent, and shifted in a negative direction in response to severe rooting ($\phi = 0.503$; CI = 0.250–0.761; Figure 5.1).

The best-supported survival model at Damdam modelled ϕ, p and r as dependent on the presence or absence of water, while turtle size positively influenced r (Table 5.1). Two similar models, each modelling ϕ, p and r as a factor of the presence or absence of water, received some degree of support (Table 5.1). Pig rooting was severe during each drying period at Damdam, and as such, the influence of pig rooting on ϕ and p could not be disentangled from drying *per se*. There was little support for modelling ϕ and p as a direct factor of harvest (Appendix Table 5.4), suggesting that, like at Giddadella, harvest did not noticeably influence ϕ and p at Damdam. Mean model averaged survival probabilities at Damdam were high between periods of inundation ($\phi = 0.831$; CI = 0.25–0.986), responding negatively to drying ($\phi = 0.396$; CI = 0.203–0.629; Figure 5.1).

Annually Dry, Rarely Harvested or Pig-impacted Billabongs: According to the most parsimonious model at Murrybulljuluk, a rare harvest event, at the end of 2003, had the greatest influence over ϕ and p, while r was influenced by the presence or absence of water

Table 5.1: Burnham-Both mark-recapture model set, showing Akaike's Information Criterion (AIC_c), number of parameters (k), deviance (Dev), change in AIC_c compared to the best-ranked model (ΔAIC_c) and model weights (w_i), for Giddadella (**a**), Damdam (**b**), Murrybulljuluk (**c**) and Little-Giddadella (**d**). Turtle size (*s*) was modelled as a covariate. Juvenile turtles (size < 140 mm) and adult and sub-adult turtles (size ≥140 mm) were grouped and treated as a grouped factor (*g*). The presence or absence of water (*wrt*) and harvesting (*h*) were treated as co-factors, as was severity of pig rooting (*rt*). Where necessary, a relative index of trapping period (*t*) averaged across all individuals in the population was modelled as an across population covariate. A time constant model (.) was also modelled. Note that only models with $w_i > 0.05$ are shown (see Appendix Table 5.4 for the complete model set).

Site	Model	AIC_c	*k*	Dev	ΔAIC_c	w_i
a	$\phi(rt)p(rt^{+}t)r(w^{+}s)f(1)$	900.82	9	882.377	0	0.418
	$\phi(rt^{+}s)p(rt^{+}s^{+}t)r(w^{+}s)f(1)$	902.503	11	879.851	1.68	0.18
	$\phi(w)p(w^{+}t)r(w^{+}s)f(1)$	903.095	9	884.653	2.28	0.134
	$\phi(rt)p(rt^{+}t)r(w)f(1)$	903.421	8	887.068	2.6	0.114
b	$\phi(w)p(w)r(w^{+}s)f(1)$	498.952	8	482.441	0	0.413
	$\phi(w^{+}g)p(w^{+}g)r(w^{+}s)f(1)$	500.197	12	475.075	1.24	0.222
	$\phi(w)p(w)r(w)f(1)$	500.796	7	486.4	1.84	0.164
	$\phi(w^{+}g)p(w^{+}g)r(w)f(1)$	502.913	11	479.967	3.96	0.057
c	$\phi(h)p(h)r(w^{+}s)f(1)$	282.156	8	265.196	0	0.648
	$\phi(h^{+}s)p(h^{+}s)r(w^{+}s)f(1)$	284.802	10	263.316	2.65	0.173
	$\phi(h^{+}g)p(h^{+}g)r(w^{+}s)f(1)$	285.471	12	259.334	3.32	0.124
d	$\phi(rt)p(rt)r(w)f(1)$	281.43	7	266.568	0	0.558
	$\phi(rt)p(rt)r(w^{+}s)f(1)$	282.761	8	265.644	1.33	0.287
	$\phi(rt^{+}s)p(rt^{+}s)r(w)f(1)$	285.956	9	266.549	4.53	0.058

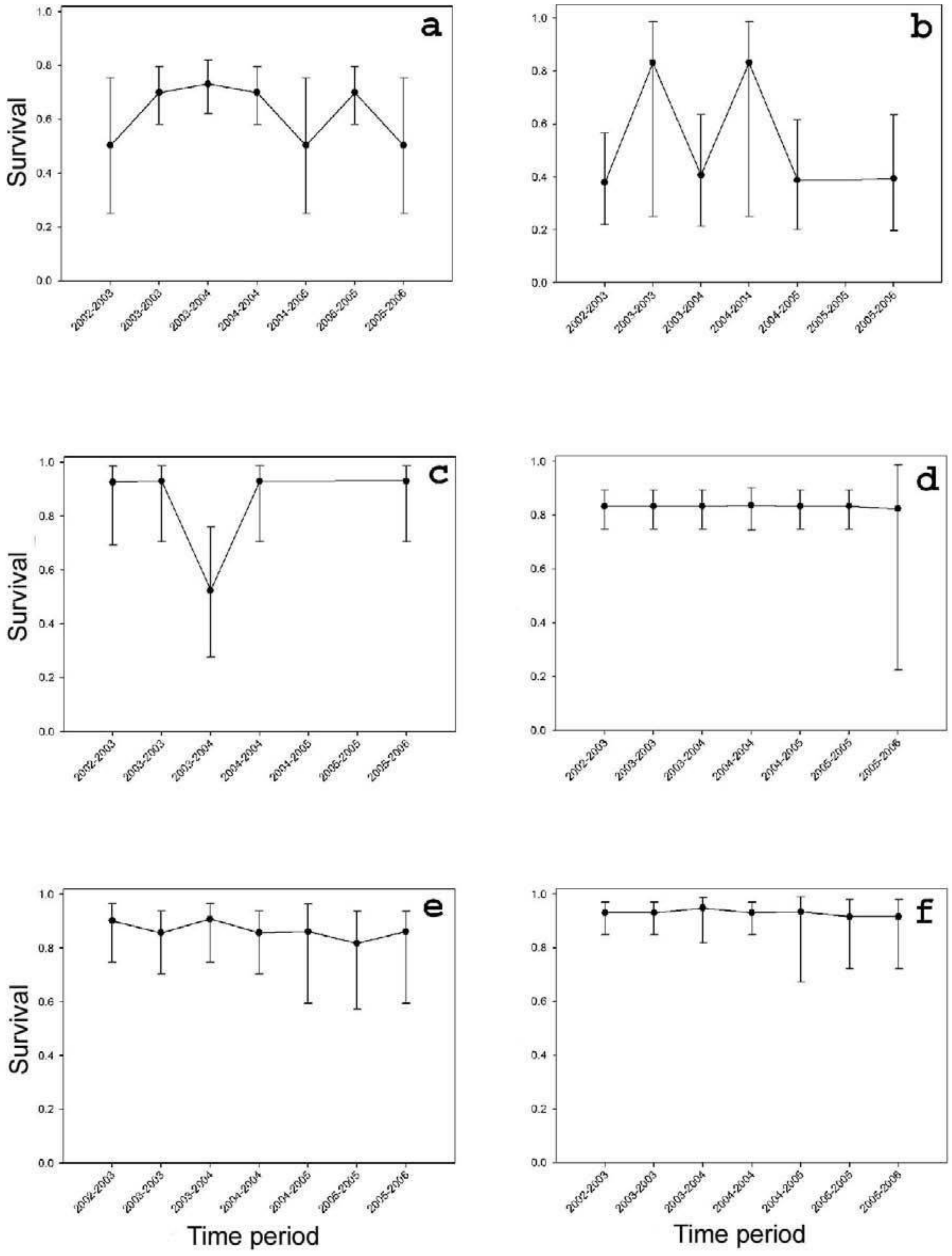


Figure 5.1: Model-averaged survival probabilities for turtles at Giddadella (**a**) and Damdam (**b**) (annually dry, harvested), Murrybulljuluk (**c**) and Little-Giddadella (**d**) (annually dry, rarely harvested), Imimbar (**e**) and Ginmilly (**f**) (rarely dry, not harvested). Note that survival at Damdam and Murrybulljuluk in 2005 could not be estimated because the billabong dried earlier than usual (see Methods).

and size (Table 5.1). There was less support for the next ranked model, which modelled ϕ and p as a factor of turtle size as well as harvest (Table 5.1). Mean model-averaged survival probabilities were high in the absence of harvest ($\phi = 0.929$; CI = 0.700–0.986), responding negatively to harvest ($\phi = 0.524$; CI = 0.276–0.76; Figure 5.1). At Little-Giddadella, the most parsimonious model established that ϕ and p were dependent on the severity of pig rooting, while the presence or absence of water influenced recovery rates (Table 5.1). A second model, similar in structure to the first but with a size effect on r, was also well supported (Table 5.1). Mean model-averaged survival probabilities at Little-Giddadella were high in the absence of heavy rooting ($\phi = 0.833$; CI = 0.746–0.895; Figure 5.1).

Rarely Dry, Unharvested, Rarely Pig-impacted Billabongs: The most parsimonious survival model at Imimbar modelled ϕ and p as dependent on size (Table 5.2; see Appendix Table 5.5 for entire model set). A model ranked lower, but not substantially so modelled ϕ and p as a factor of the monsoonal rains, as well as turtle size (Table 5.2). The mean model-averaged survival probability at Imimbar was 0.867 (CI = 0.667–0.949; Figure 5.1). Similarly, the best supported model at Ginmilly, modelled ϕ and p as dependent on size (Table 5.2). There was considerably less support for the next ranked model, which modelled ϕ and p as a factor of the monsoonal rains, as well as turtle size (Table 5.2). The mean model-averaged survival probability at Ginmilly was 0.929 (CI = 0.783–0.977; Figure 5.1).

Density Dependent Responses

Juvenile Recruitment: Hatchlings and juveniles were proportionately common in populations that experienced low adult survival during 2002–2004 (Table 5.3). In contrast, hatchlings and juveniles were proportionately rare in populations with high adult survival (Table 5.3). Notably, at Murrybulljuluk, hatchlings were absent in 2003, while in 2004, following a rare negative perturbation in density caused by harvest, hatchlings were common (Table 5.3). The correlation between periodically low survival and high hatchling and juvenile abundance suggests that hatchling recruitment increases as a response to reduction in overall population density.

Table 5.2: Cormack-Jolly-Seber mark-recapture model set showing Akaike's Information Criterion (AIC_c), number of parameters (*k*), deviance (Dev), change in AIC_c compared to the best-ranked model ($\Delta\mathrm{AIC}_c$) and model weights (w_i), for Imimbar (**a**) and Ginmilly (**b**). Turtle size (*s*) was modelled as a covariate. Juvenile turtles (size < 140 mm) and adult and sub-adult turtles (size ≥140 mm) were grouped and treated as a grouped factor (*g*). The presence or absence of monsoonal rains (*mr*) was treated as co-factors. A relative index of trapping period (*t*) averaged across all individuals in the population was modelled as an across population covariate. A time constant model (.) was also modelled. Note that only models with $w_\mathrm{i} > 0.05$ are shown (see Appendix Table 5.5 for the complete model set).

Site	**Model**	$\mathbf{AIC}_c$	***k***	**Dev**	$\mathbf{\Delta AIC_c}$	w_i
a	$\phi(s)p(s^{+} t)$	729.446	5	719.251	0	0.639
	$\phi(mr^{+} s)p(mr^{+} s^{+} t)$	730.989	7	716.621	1.54	0.295
b	$\phi(s)p(s^{+} t)$	226.825	5	216.102	0	0.748
	$\phi(mr^{+} s)p(mr^{+} s^{+} t)$	229.052	7	2130669	2.23	0.246

Table 5.3: Horvitz-Thompson population abundance estimates for hatchlings, juveniles and total population size at Giddadella (**a**), Damdam (**b**), Murrybulljuluk (**c**), Little-Giddadella (**d**), Imimbar (**e**) and Ginmilly (**f**). Approximate 95% confidence intervals are in parenthesis (see Methods).

	Site	Billabong Type	Survival 2002-2004	Hatchlings	Juveniles	Total Abundance
2003						
	a	Annually Dry, Harvested	Periodically Low	32 (24-53)	8 (6-13)	164 (118-267)
	b	Annually Dry, Harvested	Periodically Low	22 (14-48)	7 (5-16)	165 (107-372)
	c	Annually Dry, Rarely Harvested	Periodically Low	0	14 (9-27)	173 (116-331)
	d	Annually Dry, Rarely Harvested	High	0	0	34 (29-42)
	e	Rarely Dry, Unharvested	High	0	8 (6-13)	331 (237-547)
	f	Rarely Dry, Unharvested	High	0	0	51 (37-81)
2004						
	a	Annually Dry, Harvested	Periodically Low	28 (22-38)	22 (17-30)	125 (99-169)
	b	Annually Dry, Harvested	Periodically Low	14 (9-29)	10 (7-22)	147 (96-312)
	c	Annually Dry, Rarely Harvested	Periodically Low	62 (42-119)	0	179 (121-345)
	d	Annually Dry, Rarely Harvested	High	0	2 (1-2)	32 (28-40)
	e	Rarely Dry, Unharvested	High	7 (6-9)	0	243 (201-307)
	f	Rarely Dry, Unharvested	High	0	0	59 (44-87)

Size of Maturity: Minimum size of maturity for female *C. rugosa* was 182.5 mm (range = 160.4–188.2 mm; *n* = 448) and 147.9 mm for males (range = 139.9–151.9 mm; *n* = 343). Small female turtles (CL = 180–200 mm) tended to be gravid during the peak of the breeding season in populations that experienced frequent periods of low survival (Giddadella and Damdam; Figure 5.2). In contrast, females in populations with high constant survival (Imimbar and Ginmilly), or rare periods of reduced survival (Murrybulljuluk and Little-Giddadella), tended not to breed until reaching a larger size (CL > 200 mm; Figure 5.2). Median gravid turtle size at Murrybulljuluk in 2003 (251.1 mm; CI = 236.9–265.0) and 2004 (248.7 mm; CI = 233.6–263.1) remained constant despite a rare negative population perturbation late in 2003 caused by harvesting. A tendency for smaller females to be gravid in populations that frequently experience depressed survival suggests that size of maturity may be influenced by density.

Growth and Age of Maturity: With the exception of turtles at Damdam, predicted age at onset of female maturity (CL = 182.5 mm) was similar in populations that had recently experienced periods of low survival (Giddadella and Murrybulljuluk) to populations with high survival (Little-Giddadella, Imimbar, Ginmilly; Appendix Table 5.6). At Damdam predicted growth from hatching to minimum size of maturity was just 3.3 years (CI = 3.0-3.5). Mature female growth (CL > 220 mm) tended to be faster in populations that experienced periods of low adult survival during 2002 –2004 than most populations that experienced high survival (Figure 5.3). The exception was Ginmilly (high survival), where female growth was slow, but not significantly slower than at Murrybulljuluk (low survival). At Damdam and Giddadella mature female growth was fast and survival low, with turtles rarely surviving to asymptotic size (Appendix Table 5.6). Increasing female postmaturity growth in response to low survival strongly suggests a density dependent compensatory response in somatic growth rates. Male growth rates were independent of population survival; there was no correlation between population survival and age at onset of male maturity (Appendix Table 5.6). Although mature males (CL ≥ 148 mm) grew faster at Damdam, male post maturity growth did not correlate with reduced survival (Figure 5.3). Independent age estimates derived from examination of plastral annuli accorded with age estimates predicted from the growth model for male and female turtles

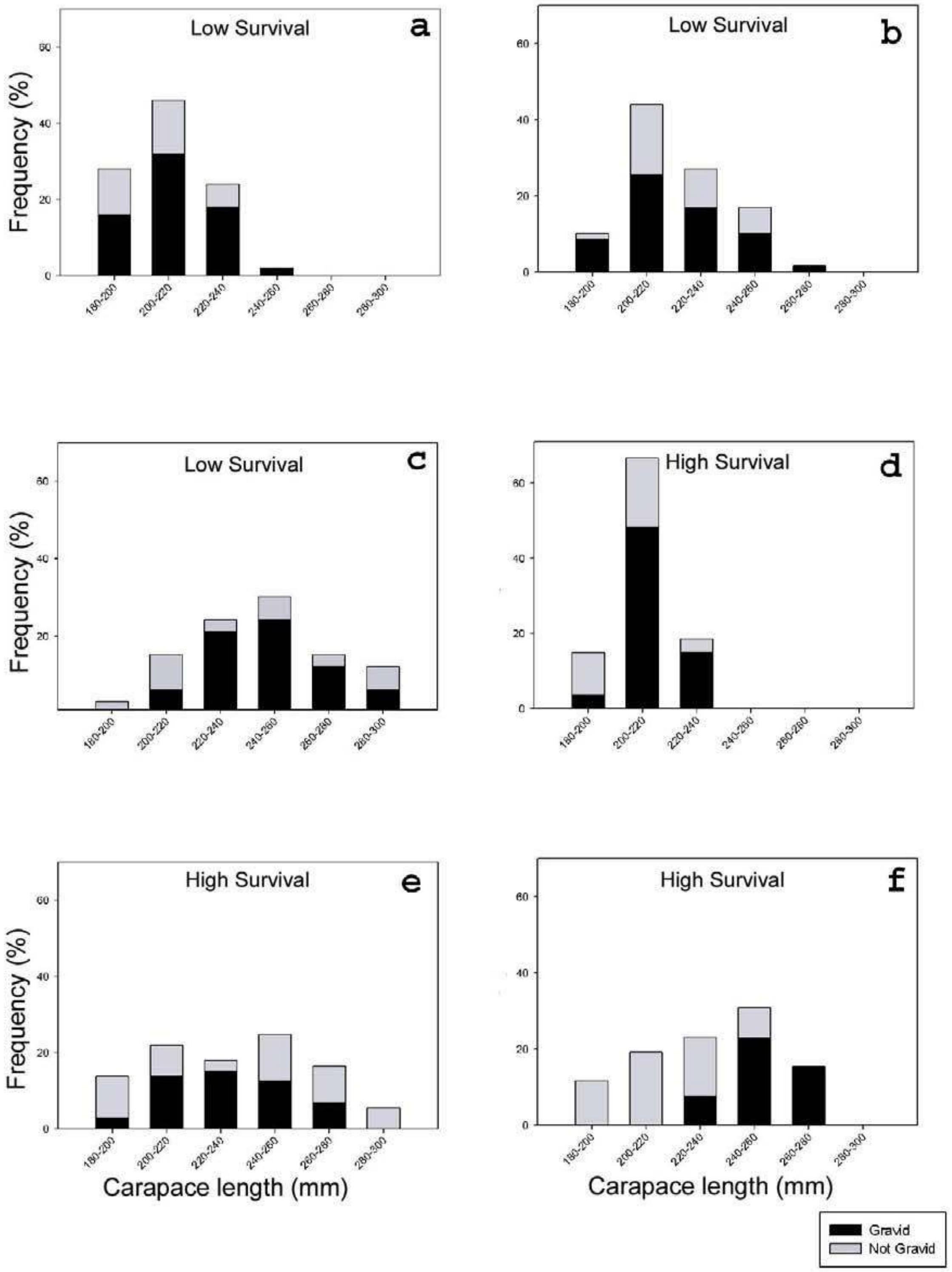


Figure 5.2: Reproductive status of female turtles during peak-breeding season. With the exception of Murrybulljuluk (**c**), small turtles (< 200 mm) tended to be gravid at populations, such as Giddadella (**a**) and Damdam (**b**), which experienced periodic low survival during 2002 – 2004. In contrast, turtles tended not to reproduce until reaching a larger size (> 200 mm) at Little-Giddadella (**d**), Imimbar (**e**) and Ginmilly (**f**), populations that experienced high survival.

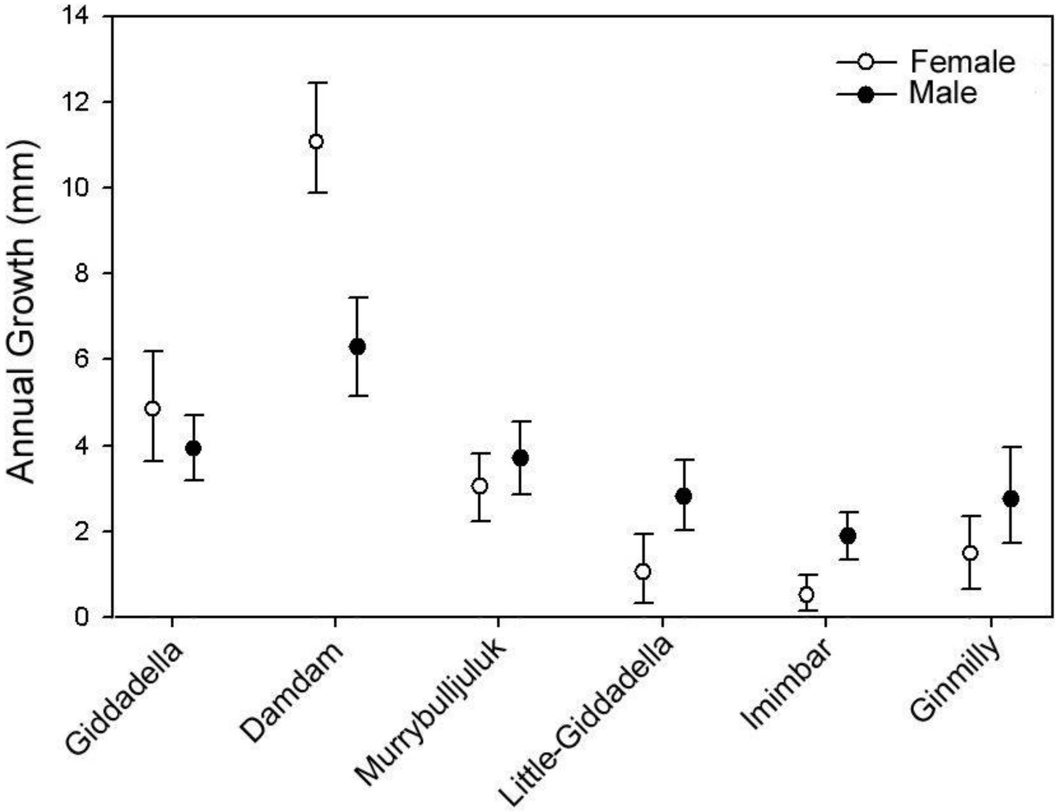


Figure 5.3: Mean post maturity growth rates (mm/yr) for females > 220 mm and males ≥ 148 mm. Mature female growth tended to be faster in populations that experienced periods of low adult survival during 2002–2004 (Giddadella, Damdam, Murrybulljuluk).

up to a size of maturity in all six populations.

Fecundity: Clutch size was strongly positively correlated with body size. Based on the evidence ratio (*ER*, ratio of w_i between two models), the linear model was 1.35×10^{19} times better supported by the data than the null model. Clutch size and clutch mass, adjusted for body size, did not correlate with population survival. The most parsimonious model had clutch size as a function of population of origin (*clutch = population*; w_i = 0.702). There was little support for the global model (Δ_i = 2.45; w_i = 0.206) and the model *clutch = survival* (Δ_i = 4.06; w_i = 0.092), and no support for the null model (Δ_i = 17.67; w_i = 0.001). The null model was the most parsimonious model for clutch mass (w_i = 0.518). The models, *mass = population* (Δ_i = 1.69; w_i = 0.217) and *mass = survival* (Δ_i = 1.70; w_i = 0.216) were ranked lower, but not substantially so, and there was little support for the global model (Δ_i = 4.14; w_i = 0.064). Turtles in populations with high and low survival tended to lay 3–4 clutches annually, although in some years turtles probably laid only two clutches, while in other years turtles may have laid up to 5 clutches (Appendix Table 5.7).

Discussion

Density dependent processes are a pervasive feature of the population dynamics of most organisms (Rose *et al.* 2001; Brook & Bradshaw 2006), but the degree to which they can compensate for chronic increases in mortality, especially in long-lived taxa, remains unclear (Pöysä *et al.* 2004). The harvesting of freshwater turtles has been widely criticised because their life history attributes and population dynamics are thought to make them particularly vulnerable to off-take (Cunnington & Brooks 1996; Heppell 1998). In particular they have been presumed to be unable to respond to harvest through density dependent compensatory processes (Congdon *et al.* 1993, 1994). Life history traits may directly influence population persistence under conditions of reduced survival caused by harvest (Smith et al. 1998). Species that mature late, experience high levels of survival and have a long generation times are more vulnerable to overexploitation, than species with higher fecundity and more rapid turnover of generations (Musick *et al.* 2000). *Chelodina rugosa* is fast growing, highly fecund and early maturing compared to other turtles (Kennett 1996, 1999) making *C. rugosa* better suited to cope with frequent episodes of low survival than chelonians that have been previously studied. Moreover, our analysis strongly suggests that *C. rugosa* has the capacity to compensate for low rates of adult survival via increases in juvenile survival, decreases in size of maturity and increases in postmaturity growth; in turn promoting an increase in juvenile recruitment and age-specific fecundity.

An interaction between density and juvenile survival has been established for birds (Sedinger, Lindberg & Chelgren 2001), mammals (Fowler 1987; Gaillard *et al.* 1998), reptiles (Massot *et al.* 1992) and fish (Rose *et al.* 2001). At high densities, the survival of small individuals may be depressed owing to low per capita resource availability during reproduction (Choquenot 1991), or increased resource competition after birth or hatching (Sedinger *et al.* 1998). Alternatively cannibalism (adults eating their young) can result in strong density dependent feedback in juvenile survival, as documented in a variety of fish species (Rose *et al.* 2001). In *C. rugosa*, low sub-adult and adult survival appears to elicit increased hatchling survival and in turn increased juvenile recruitment. Hatchlings and juveniles (CL < 140 mm) were well represented at populations that experienced episodes of low survival during 2002–2004 (Giddadella, Damdam and Murrybulljuluk), compared to those that experienced relatively higher rates of survival (Little-Giddadella, Imimbar and Ginmilly; Table 5.3). Juvenile abundance provides a good proxy for hatchling recruitment (Madsen and Shine 2000), particularly given that turtle mortality at harvested billabongs was not size dependent in *C. rugosa*. Furthermore size positively influenced *C. rugosa* survival at rarely drying billabongs (populations with high overall survival; Table 5.2). This finding is consistent with the hypothesis that *C. rugosa* populations are regulated by density, which negatively influences the recruitment of small individuals into the larger size classes.

A density dependent interaction between somatic growth, body condition and age-specific fecundity may arise when animal size, or nutritional status, rather than age, dictate maturity (Jorgenson *et al.* 1993; Festa-Bianchet, Gaillard & Jorgenson 1998). Alternatively, increasing age-specific fecundity in response to low survival may result from a decrease in size of maturity (Abrams & Rowe 1996). Small, gravid turtles (carapace length < 200 mm) were relatively common during peak-breeding season in populations that frequently experience periods of low survival (Giddadella and Damdam) compared to populations where survival remained high (Figure 5.2). In maturing at a smaller size in populations with low survival, age-specific fecundity increased without a concomitant increase in juvenile and sub-adult growth. Since female reproductive size at Murrybulljuluk did not decline in response to a rare period of low survival in 2003, decreased size of maturity may be a local adaptation – an evolved response that promotes demographic resilience, and therefore persistence, under conditions of comparatively low survival (Bronikowski and Arnold 1999). To clarify this assertion, manipulative studies are needed to test experimentally the processes that promote a reduction in size of maturity in response to reduced survivorship.

In populations with relatively high survival probabilities, male and female *C. rugosa* grow rapidly to maturity, whereupon growth becomes slow and indeterminate (Kennett 1996). In contrast, females in populations with low survival continue to grow vigorously after reaching maturity (Figure 5.3). Clutch size is directly related to body size in *C. rugosa* (see Results); thus, a fast rate of post maturity growth increases age-specific fecundity in response to reduced survival. Conversely, post maturity growth in males, who invest relatively fewer resources in reproduction, is not strongly influenced by population survival probabilities (Figure 5.3). Size does not enhance *C. rugosa* survival under conditions of high pig predation and harvest (Table 5.1). Hence, a compensatory increase in age-specific fecundity is the only plausible explanation for accelerated female post maturity growth in populations where survival probabilities are low.

Clutch size and mass may decline with increasing density (Massot *et al.* 1992), though this was not the case for *C. rugosa*. Although clutch size was influenced by site of capture, neither clutch size nor clutch mass (adjusted for body size) were influenced by survival rate. Annual clutch frequency did not vary with survival; rather, turtles tended to produce 3-4 clutches each year, irrespective of survival probabilities (Appendix Table 5.7). The absence of any interaction between survival probabilities and either clutch size, or clutch frequency, is explicable if one considers that reproduction in *C. rugosa* is timed to coincide with a period of high food availability (Fordham, Georges and Corey 2006a).

Pig abundance had the largest impact on *C. rugosa* survival. The strongest compensatory response, indicated by the correlation analysis, occurred in populations where pig abundance was high and thus rooting severe (Damdam and Giddadella). These populations were distinguished by high juvenile recruitment, early onset of maturity, and fast post maturity growth. As such, our monitoring evidence indicates that compensatory density-related responses play an important role in promoting population persistence in *C. rugosa* under conditions of heavy pig predation. The interaction between pig abundance and *C. rugosa* survival is complex, being related to prominent vegetation type and timing of drying. Murrybulljuluk is devoid of *Eleocharis*, a seasonal dietary staple for pigs (Fordham *et al.* 2006b), and thus, pig abundance is low, and turtle survival probabilities high (in the absence of harvesting), despite frequent drying (Figure 5.1). In 2003 Giddadella dried later than in previous years (i.e., November, rather than June–August), forcing pigs to congregate around more permanent water sources, leading to low pig abundance and high consequent turtle survival (Figure 5.1). Conversely, in 2005 Little-Giddadella dried earlier than usual (August rather than November – December) causing high pig abundance, negatively impacting turtle survival.

With the exception of harvesting at Damdam in 2002, harvest rates were low at sites where pig abundance was high. In 2002, indigenous harvesters at Damdam discarded traditional harvest techniques that restrict them to a dry environment, and harvested immediately before, and during, the early aestivation period, when pig predation is high, providing an improved harvest yield in the face of this predator competition. Only 35 years ago, *C. rugosa* yields were relatively high in Arnhem Land (Russell-Smith *et al.* 1997) and pigs were in all probability locally rare or non-existent, because pig meat was rarely consumed (Altman 1984). We infer that turtle harvesting would have been at least partially compensated through density dependent responses. Harvesting in 2003 at Murrybulljuluk, where pig abundance is low, caused a marked decline in survival (Figure 5.1), which correlated with increased hatchling recruitment in 2004 (Table 5.3), signalling a compensatory response to harvest.

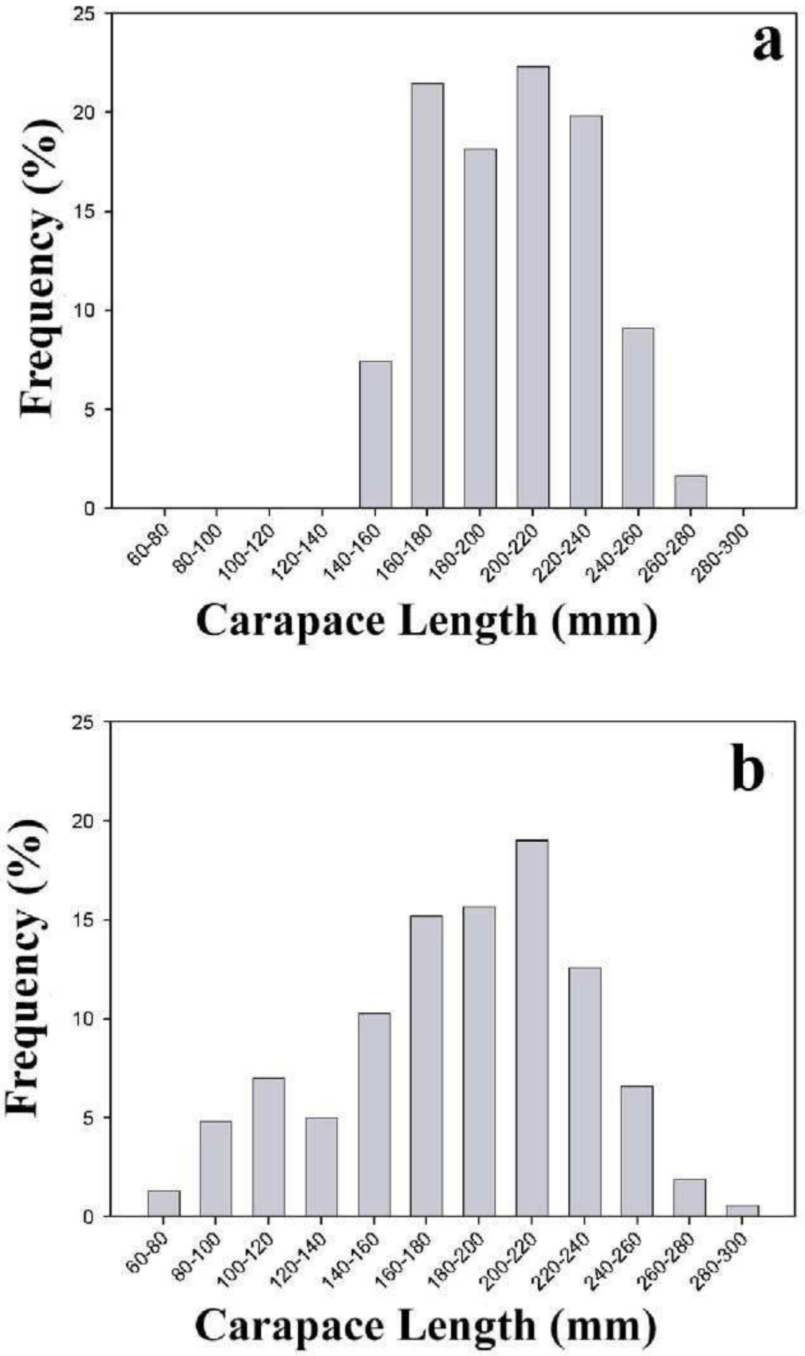
To our knowledge, this is the first experimentally replicated study to comprehensively demonstrate a correlation between compensatory responses and periodic low adult survival in a turtle species. The significance of these findings are broad, challenging the prevailing view that sustained high post hatchling survival is crucial for achieving long-term population stability in chelonians (Brooks *et al.* 1991b; Congdon *et al.* 1993, 1994; Doak, Kareiva & Klepetka 1994; Heppell *et al.* 1996; Heppell 1998; Chaloupka 2002; Converse *et al.* 2005). Our capture-mark-recapture evidence suggests that chelonians with life history traits similar to *C. rugosa* may persist periods of low post hatchling survival via a range of density dependent compensatory responses. Rock art and ceremonial stories indicate that *C. rugosa* populations have survived many millennia of traditional harvesting (Chaloupka 1993), and it is reasonable to assume that compensatory strategies such as those described in this paper are responsible for population persistence in *C. rugosa* over this long period of interaction with people in tropical northern Australia.

Although survival probabilities that varied across billabongs provided opportunity to infer density dependent compensatory responses in *C. rugosa*, there are limitations to inferring causality from correlation. There remains a need to conclusively demonstrate density dependent responses, ideally through experimental manipulations of population size.

Appendices

Appendix 5.1: Detailed Trapping and Measurement Procedures. Each population was trapped twice per year, from 2002 to 2005, using fyke nets made from 5 ply net with a 12 mm mesh size. Fyke net arm length was 20 m with a 2.5 m drop. Trapping occurred once at the end of the wet season (April-May) and once at the end of the dry season (September-October), or immediately before drying, whichever occurred first. In 2005, Damdam and Murrybulljuluk dried earlier than usual which restricted trapping while in 2006, turtles were caught only once at the end of the wet season. Where possible, each trapping event consisted of 20 trapping nights. Fyke nets were checked at 4-7 day intervals. Each animal caught was weighed with an electronic field balance (± 0.01 g) and its straight-line maximum carapace length (CL) was measured with callipers (± 0.01 mm). Plastral annuli were recorded for estimation of age (Kennett 1996) and to complement direct measurements of growth (Georges, Guarino & White 2006b). Periodicity of annuli was confirmed for immature and fast growing adult *C. rugosa* by repeated annual examination of growth annuli from recaptured individuals (Fordham unpublished data). Hatchlings were identified by the absence of annuli and the presence of a hatchling scute.

Sex of mature animals was determined by examination of the tail, which is markedly longer and thicker in mature males than in mature females (Kennett 1999; Georges *et al.* 2006b). The relationship between body size and basal thickening of the tail was used to estimate male size at the onset of maturity. Minimum size of male maturity was calculated as the average size of the 20 smallest male turtles that exhibited basal thickening of the tail (male turtles, $n = 343$). Animals smaller than the smallest identifiable male (< 140 mm) that had experienced one full growth season were for operational purposes classified as juveniles. Each female turtle was palpated for eggs. Female minimum size of maturity was calculated as the average of the 20 smallest gravid females (gravid turtles, $n = 448$). Females ≥ 140mm, but smaller than the smallest mature female, were classed as sub-adults. The presence or absence of eggs during the peak of the breeding season (April-May) was used to assess the proportion of adults that were reproductive (Madsen and Shine 2000). Gravid turtles were X-rayed to reveal clutch size according to published protocols (Gibbons and Greene 1979). Turtles were marked following Georges *et al.* (2006b) and released at site of capture. A sample of six gravid turtles were caught and dissected each year at each billabong to remove the gonads. Three turtles were caught early-mid breeding season (May-June), and three were caught at the end of the breeding season, either immediately before drying or during the mid-late dry season (August-September), whichever came first. Gonads were examined according to procedures outlined by Georges (1983) to determine annual clutch frequency. The eggs collected from dissected turtles were measured (± 0.01 mm) and weighed (± 0.01 g). Eggs were also collected by inducing gravid turtles to lay eggs with an intra-muscular injection of synthetic hormone Oxytocin® at a dosage rate of 1 unit/100 g body mass (Ewert and Legler 1978). Clutch size and mass in *C. rugosa* are positively correlated with female body size (Kennett 1999). The effects of body size were removed by regression analysis. Specifically we used the natural log of clutch size and mass regressed on the natural log of carapace length to calculate size-adjusted data (Iverson *et al.* 1993).



Appendix Figure 5.4: Pooled size distribution of harvested turtles (**a**) and trapped turtles (**b**) at Giddadella, Damdam and Murrybulljuluk billabongs. Harvesting by indigenous people targets sub-adult and adult turtles (carapace length ≥ 140 mm).

Appendix Table 5.4: Entire Burnham-Both mark-recapture model set showing Akaike's Information Criterion (AIC_c), number of parameters (k), deviance (Dev), change in AIC_c compared to the best-ranked model (ΔAIC_c) and model weights (w_i), for Giddadella (**a**), Damdam (**b**), Murrybulljuluk (**c**), Little-Giddadella (**d**). See Table 5.1 for a description of model variables.

Site	Model	AIC_c	k	Dev	ΔAIC_c	w_i
a	$\phi(rt)p(rt^{+}t)r(w^{+}s)f(1)$	900.82	9	882.377	0	0.418
	$\phi(rt^{+}s)p(rt^{+}s^{+}t)r(w^{+}s)f(1)$	902.503	11	879.851	1.68	0.18
	$\phi(w)p(w^{+}t)r(w^{+}s)f(1)$	903.095	9	884.653	2.28	0.134
	$\phi(rt)p(rt^{+}t)r(w)f(1)$	903.421	8	887.068	2.6	0.114
	$\phi(rt+s)p(rt^{+}s^{+}t)r(w)f(1)$	905.441	10	884.899	4.62	0.041
	$\phi(w)p(w^{+}t)r(w)f(1)$	905.665	8	889.312	4.85	0.037
	$\phi(w^{+}s)p(w^{+}s^{+}t)r(w^{+}s)f(1)$	905.991	11	883.339	5.17	0.032
	$\phi(rt^{+}g)p(rt^{+}g^{+}t)r(w^{+}s)f(1)$	906.206	14	877.161	5.39	0.028
	$\phi(w^{+}s)p(w^{+}s^{+}t)r(w)f(1)$	909.102	10	888.56	8.28	0.007
	$\phi(w^{+}g)p(w^{+}g^{+}t)r(w^{+}s)f(1)$	909.485	14	880.44	8.67	0.006
	$\phi(rt^{+}g)p(rt^{+}g^{+}t)r(w)f(1)$	910.968	13	884.065	10.15	0.003
	$\phi(w^{+}g)p(w^{+}g^{+}t)r(w)f(1)$	911.584	13	884.681	10.76	0.002
	$\phi(s)p(s)r(s)f(1)$	963.996	7	949.722	63.18	0
	$\phi(.)p(.)r(.)f(1)$	964.597	4	956.5	63.78	0
b	$\phi(w)p(w)r(w^{+}s)f(1)$	498.952	8	482.441	0	0.413
	$\phi(w^{+}g)p(w^{+}g)r(w^{+}s)f(1)$	500.197	12	475.075	1.24	0.222
	$\phi(w)p(w)r(w)f(1)$	500.796	7	486.4	1.84	0.164
	$\phi(w^{+}g)p(w^{+}g)r(w)f(1)$	502.913	11	479.967	3.96	0.057
	$\phi(w^{+}s)p(w^{+}s)r(w^{+}s)f(1)$	503.224	10	482.438	4.27	0.049
	$\phi(h)p(h)r(w^{+}s)f(1)$	503.233	8	486.722	4.28	0.049
	$\phi(w^{+}s)p(w^{+}s)r(w)f(1)$	505.027	9	486.387	6.08	0.02
	$\phi(h^{+}s)p(h^{+}s)r(w^{+}s)f(1)$	505.943	10	485.157	6.99	0.013
	$\phi(h^{+}s)p(h^{+}s)r(w)f(1)$	507.838	9	489.197	8.89	0.005
	$\phi(h^{+}g)p(h^{+}g)r(w^{+}s)f(1)$	507.889	12	482.767	8.94	0.005
	$\phi(h)p(h)r(w)f(1)$	507.945	7	493.549	8.99	0.005
	$\phi(h^{+}g)p(h^{+}g)r(w)f(1)$	511.379	11	488.433	12.43	0.001
	$\phi(.)p(.)r(.)f(1)$	535.271	4	529.187	36.32	0
	$\phi(s)p(s)r(s)f(1)$	537.572	7	523.176	38.62	0

c	$\phi(h)p(h)r(w+s)f(1)$	282.156	8	265.196	0	0.648
	$\phi(h+s)p(h+s)r(w+s)f(1)$	284.802	10	263.316	2.65	0.173
	$\phi(h+g)p(h+g)r(w+s)f(1)$	285.471	12	259.334	3.32	0.124
	$\phi(h+s)p(h+s)r(w)f(1)$	287.418	9	268.21	5.26	0.047
	$\phi(w)p(w)r(w+s)f(1)$	291.696	8	274.736	9.54	0.006
	$\phi(w+g)p(w+g)r(w+s)f(1)$	294.482	12	268.345	12.33	0.001
	$\phi(w+s)p(w+s)r(w+s)f(1)$	294.744	10	273.258	12.59	0.001
	$\phi(h)p(h)r(w)f(1)$	297.325	7	282.583	15.17	0
	$\phi(h+g)p(h+g)r(w)f(1)$	298.006	11	274.21	15.85	0
	$\phi(w+s)p(w+s)r(w)f(1)$	300.277	9	281.069	18.12	0
	$\phi(w+g)p(w+g)r(w)f(1)$	307.049	11	283.253	24.89	0
	$\phi(w)p(w)r(w)f(1)$	309.895	7	295.153	27.74	0
	$\phi(s)p(s)r(s)f(1)$	323.209	7	308.468	41.05	0
	$\phi(.)h(.)r(.)f(1)$	343.543	4	335.284	61.39	0
d	$\phi(rt)p(rt)r(w)f(1)$	281.43	7	266.568	0	0.558
	$\phi(rt)p(rt)r(w+s)f(1)$	282.761	8	265.644	1.33	0.287
	$\phi(rt+s)p(rt+s)r(w)f(1)$	285.956	9	266.549	4.53	0.058
	$\phi(rt+s)p(rt+s)r(w+s)f(1)$	287.338	10	265.605	5.91	0.029
	$\phi(w)p(w)r(w)f(1)$	287.89	7	273.028	6.46	0.022
	$\phi(rt+g)p(rt+g)r(w)f(1)$	287.9	11	263.805	6.47	0.022
	$\phi(w)p(w)r(w+s)f(1)$	289.392	8	272.276	7.96	0.01
	$\phi(rt+g)p(rt+g)r(w+s)f(1)$	289.776	12	263.28	8.35	0.009
	$\phi(w+s)p(w+s)r(w)f(1)$	291.643	9	272.236	10.21	0.003
	$\phi(w+s)p(w+s)r(w+s)f(1)$	293.458	10	271.726	12.03	0.001
	$\phi(w+g)p(w+g)r(w)f(1)$	295.21	11	271.115	13.78	0.001
	$\phi(w+g)p(w+g)r(w+s)f(1)$	297.289	12	270.793	15.86	0
	$\phi(.)p(.)r(.)f(1)$	299.796	4	291.496	18.37	0
	$\phi(s)p(s)r(s)f(1)$	305.076	7	290.215	23.65	0

Appendix Table 5.5: Entire Cormack-Jolly-Seber mark-recapture model set showing Akaike’s Information Criterion (AIC_c), number of parameters (k), deviance (Dev), change in AIC_c compared to the best-ranked model (ΔAIC_c) and model weights (w_i), for Imimbar (**a**) and Ginmilly (**b**). See Table 5.2 for a description of model variables.

Site	**Model**	**AIC_c**	***k***	**Dev**	**ΔAIC_c**	**w_i**
a	$\phi(s)p(s^{+}t)$	729.446	5	719.251	0	0.639
	$\phi(mr+s)p(mr+s+t)$	730.989	7	716.621	1.54	0.295
	$\phi(mr)p(mr+t)$	735.767	5	725.571	6.32	0.027
	$\phi(.)p(t)$	735.945	3	729.868	6.5	0.248
	$\phi(g)p(g^{+}t)$	737.112	5	726.917	7.67	0.014
b	$\phi(s)p(s^{+}t)$	226.825	5	216.102	0	0.748
	$\phi(mr+s)p(mr+s+t)$	229.052	7	2130669	2.23	0.246
	$\phi(.)p(t)$	237.114	3	230.831	10.29	0.004
	$\phi(mr)p(mr+t)$	239.996	5	229.273	13.17	0.001
	$\phi(g)p(g^{+}t)$	240.475	5	229.753	13.65	0.001

Appendix Table 5.6: von Bertalanffy growth parameter (*k*), asymptotic size, age of maturity, postmaturity growth and percentage of turtles caught of asymptotic size at Giddadella (**a**), Damdam (**b**), Murrybulljuluk (**c**), Little-Giddadella (**d**), Imimbar (**e**) and Ginmilly (**f**). Note that female post maturity growth is calculated using growth data from females with CL > 220 mm, while female age of maturity is based on minimum size of maturity (182.5 mm). Male post maturity growth and age of maturity is calculated using minimum size of male maturity (CL ≥ 148 mm)

	Site	Billabong Type	Survival 2003-2004	*k*	Asymptotic Size (mm)	Age of Maturity (yrs)	Postmaturity Growth (mm/yr)	Assymptotic Turtles (%)
Female								
	a	Annually Dry, Harvested	Periodically Low	0.293 (0.239 - 0.347)	236.9 (219.6 -254.1)	4.9 (4.6 - 5.5)	4.85 (3.64 - 6.19)	4.6 (n = 87)
	b	Annually Dry, Harvested	Periodically Low	0.303 (0.268 - 0.339)	270.4 (257.1 - 283.6)	3.3 (3 - 3.5)	11.07 (9.89 - 12.44)	1 (n = 105)
	c	Annually Dry, Rarely Harvested	Periodically Low	0.24 (0.215 - 0.265)	250.2 (239.6 - 260.8)	5 (4.5 - 5.6)	3.04 (2.23 - 3.8)	39.2 (n = 56)
	d	Annually Dry, Rarely Harvested	High	0.343 (0.298 - 0.387)	226.8 (216.4 - 226.8)	5.9 (4.6 - 9)	1.06 (0.34 - 1.94)	18.3 (n = 60)
	e	Rarely Dry, Unharvested	High	0.219 (0.197 - 0.242)	246.5 (240.6 - 252.4)	6 (4.8 - 7.7)	0.52 (0.14 -0.99)	44.7 (n = 170)
	f	Rarely Dry, Unharvested	High	0.212 (0.194 - 0.23)	254.4 (248.3 -260.5)	5.5 (5 - 6.1)	1.49 (0.65-2.35)	32.5 (n = 43)
Male								
	a	Annually Dry, Harvested	Periodically Low	0.366 (0.333 - 0.399)	185.3 (179.4 - 191.1)	3.8 (3.6 - 4.3)	3.93 (3.18 - 4.69)	20.5 (n = 83)
	b	Annually Dry, Harvested	Periodically Low	0.45 (0.403 - 0.496)	188.9 (181.9 - 195.8	3 (2.8 - 3.3)	6.29 (5.14 - 7.44)	17.2 (n = 93)
	c	Annually Dry, Rarely Harvested	Periodically Low	0.372 (0.332 - 0.412)	192.4 (184.3 -200.5)	3.5 (3.2 - 3.9)	3.71 (2.87 - 4.57)	43.9 (n = 41)
	d	Annually Dry, Rarely Harvested	High	0.48 (0.409 -0.552)	177.6 (172.9 - 182.4)	2.8 (2.2 - 4)	2.82 (2.02 - 3.66)	34.4 (n = 32)
	e	Rarely Dry, Unharvested	High	0.393 (0.348 - 0.437)	190 (185.9 - 194.2)	3.8 (3 - 5.5)	1.88 (1.35 - 2.44)	31.1 (n = 106)
	f	Rarely Dry, Unharvested	High	0.279 (0.248 - 0.31)	201.6 (194.7 - 208.5)	4.4 (3.8 - 5.4)	2.75 (1.74 - 3.96)	34.7 (n =23)

Appendix Table 5.7: Seasonal occurrence of corpora lutea and ovarian follicles of various sizes for *Chelodina rugosa* at Giddadella (**a**), Damdam (**b**), Murrybulljuluk (**c**), Little-Giddadella (**d**), Imimbar (**e**), Ginmilly (**f**). Potential clutches are highlighted in yellow. Note that turtles in populations with high and low survival tended to lay 3–4 clutches annually.

Site	Billabong Type	Survival	Month	Year	Corpora Lutea Size Classes	Potential Future Clutches	Ovarian Follicles (Diameter in mm)																				Oviducle Eggs
							1_3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
a	Annually Dry, Harvested	Periodically Low	May	2003	1	2	55			1	2	1	1	2	1			2	1	2	7	2						13
			May	2003	2	2	80	5		1			1	2		1		5			8	7						16
			May	2003	2	2	40	9	2	1	1		1		1		4			1	1	13						12
			July	2003	3	0	38							1					1			5	1					14
			July	2003	3	2	36	13	3	2		3	3	1				1	3	2		3	2					10
			July	2003	3	1	37			1											2	7	1					11
			May	2004	2	2	34	3		1	2	2		1	2		3	2		7	4	2						11
			May	2004	1	2	68	4	1		1		1	1	1	1	1	1		4	2	3						9
			May	2004	2	2	33	10	6	1	4	2		2		2		1	2	5								9
			July	2004	3	0	26	6	1	1	1			1	1													14
			July	2004	3	0	6	2	2																			12
			July	2004	3	0	11																					8
b	Annually Dry, Harvested	Periodically Low	June	2003	2	2	43	2	4	2	5	1	1	2		2	4		1	5								10
			June	2003	2	2	59	3		2	1	5	3	1			1	6	5									8
			June	2003	2	2	35	7	2	1	4	1	4			1	5	3	2	1								12
			Aug	2003	3	1	52		6	1					5		1	2	3	7	4							17
			Aug	2003	3	1	28	3	4	3	3						2	3	2	3								7
			Aug	2003	3	1	18		1			1	3	2	1						3							5
			June	2004	2	1	54		3	1	1		1	2	3	4	6	2										11
			June	2004	2	2	41	4				2	4		2	1			1	8	2							12
			June	2004	2	2	19	2		3	1	3	3	1	3			1	3	6	3		1					14
			Sep	2004	2	0	37																					
			Sep	2004	3	0	28	1	2	1		1	3	3		1												
			Sep	2004	3	0	32	2		2	3	3	5	2	2	8		1										
c	Annually Dry, Rarely Harvested	Periodically Low	May	2003	2	2	40	4	4	6	1	1	1	1	1	1			2		1	8						14
			May	2003	2	3	91	19	3	3	1	4	1	2		2	2	3	4	1	2			13	1			18
			May	2003	2	2	68	12	2	11										3	2	2	1	1				14
			August	2003	3	0	38	10			3	5							1		2	4						17
			August	2003	3	0	20	8		1		1	2	1								2						12
			August	2003	3	0	21					1																14
			May	2004	1	2	26	8	1		4	5	2	4	4	1	2		11	4	2	3						22
			May	2004	2	0	16	4	1	1		1																10
			May	2004	1	3	117	11	7	8	1	8		8	2	5	3	1				4	7	8				18
			August	2004	3	0	32																					
			August	2004	2	0	27																					
			August	2004	3	0	11																					
d	Annually Dry, Rarely Harvested	High	May	2003	1	1	36	2	1	1				1		1			1	1				7	1			9
			May	2003	2	2	30	12	2	1	1	1				1	2	1	3	1	2							11
			May	2003	1	3	43	6	1	5	2	1	1			2	3	2	2	1			2	8				10
			Sep	2003	2	0	21	1																				
			Sep	2003	2	0	19		1																			
			Sep	2003	2	0	7			1		1																
			May	2004	2	1	23					1		1	1						1	8	1					10
			May	2004	2	1	26	7	2	1		2			2	2		2	1									9
			May	2004	1	1	32									2	1				2	4		2				11
			Aug	2004	2	0	18											1	3	2								
			Sep	2004	1	0	42			3	2				2													
			Sep	2004	2	0	23	1		1																		
e	Rarely Dry, Unharvested	High	May	2003	1	3	61	9		6	2	2	2	1		2	5	2	2				2	10	1			15
			May	2003	2	2	35	5	1	4	1	1	2	3		1		1	2	5	6							18
			May	2003	1	3	42	11	2	3	1	5			3	1	1	4	7				1	9	1			11
			Aug	2003	3	2	35	3	2	2	1	1	3					1	2		1	2	1	1				10
			Aug	2003	3	1	21	1																10				11
			Aug	2003	3	0	31	2		4		2			1			1										13
			May	2004	2	3	62	4	1	3		1		5		2	1		1	8	2				3	1	5	10
			May	2004	2	3	48	1		4	1	4		1		2	3	1	1		5		3	7	4	2		12
			May	2004	1	2	49	4	1	2		3	2		1	4	3		2		5	4						10
			Sep	2004	3	0	21						1															14
			Sep	2004	2	0	11																					
			Sep	2004	3	0	19			2			1															11
f	Rarely Dry, Unharvested	High	May	2003	2	2	98			1	1			1			1	1	1	2	5	10		17	3			21
			May	2003	2	2	52	7	6	2	1	2		4	1	4	3	2				1	12	7	1			19
			May	2003	3	0	23	2	1	2		1																14
			Sep	2003	2	0	13																					
			Sep	2003	2	0	56		1	3	4																	
			Sep	2003	1	0	6																					
			May	2004	2	2	43	5	1	1	4	2	5						1	4	2	8						18
			May	2004	2	2	31	3	1	1	3	3		3		1		1	4		4	5						14
			May	2004	2	2	39		2	2	4	2	4	2						2	2	5	7					15
			Sep	2004	1	0	2				1	7	2															
			Sep	2004	1	0	14																					
			Sep	2004	1	0	13		2	2	1																	

Experimental evidence for density dependent responses to indigenous harvest and pig predation of snake-necked turtles.

Turtle harvesting on Gunbalanya flood plain [A. Georges]

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Summary

Density dependent compensation has rarely been demonstrated in long-lived reptiles. We used an experimental manipulation of population density in six replicate wild populations of the northern snake-necked turtle (*Chelodina rugosa*) to show that this species is able to rebound rapidly following reductions in density, thereby providing resilience to harvest and pig predation. Remarkably, in some populations, turtle abundance took as little as one year to recover from a strong negative perturbation (>50% population reduction) in sub-adult and adult density, owing to increased hatchling recruitment and survival into larger size classes. These results challenge the general perceptions that freshwater turtles are highly susceptible to any form of off-take and that high sub-adult and adult survival is crucial for achieving long-term population stability in freshwater turtles. We argue against a universal generality on turtle vulnerability to sub-adult and adult harvesting. In the case of *C. rugosa*, generalities would produce overly cautious prescriptions for sustainable management.

Introduction

Density dependent processes afford the resilience required for populations to recover rapidly from downward displacement of population numbers, and they afford resistance to chronic depression of abundance that would otherwise occur from sustained increases in mortality in a wide range of organisms (Brook and Bradshaw 2006), including long-lived vertebrates (Fowler 1987; Gaillard *et al.* 1998). For freshwater turtles, however, the prevailing perception is that density dependent responses are weak or non-existent (Brooks *et al.* 1991b; Congdon *et al.* 1993 & 1994). In contrast, some turtle populations are known to have persisted over a long period of subsistence exploitation (Fordham *et al.* 2006b).

Freshwater turtles tend to have a life history strategy characterised by high fecundity (compared to other amniotes), low hatchling survival, delayed maturity, high juvenile and adult survival, and potentially long lifespans (Heppell 1998). As such, harvesting adult and sub-adult turtles is thought to jeopardise population persistence, because it is the older individuals that have the highest reproductive value (Congdon *et al.* 1993 & 1994; Cunnington & Brooks 1996). Although high rates of survival are certainly crucial for the persistence of some chelonians (Doak *et al.* 1994; Heppell 1998; Chaloupka 2002), the generality of this statement has been challenged for turtles (Fordham *et al.* 2007) and for other long-lived organisms, such as condrichthyans, which exhibit differential vulnerability to exploitation (Steven *et al.* 2000). Work on multiple populations of the northern snake-necked turtle (*Chelodina rugosa*) has established a correlation between the intensity of sub-adult and adult turtle mortality (caused by pig predation and indigenous harvesting) and key life history parameters. These correlations indicate that *C. rugosa* may compensate for low rates of sub-adult and adult survival via (i) increases in hatchling survival, (ii) decreases in female size of maturity and (iii) increases in post-maturity growth (Fordham *et al.* 2007).

The ephemeral swamps and other wetlands of the wet-dry tropics of northern Australia supports high densities of *C. rugosa*. Turtle activity is punctuated each year by the dry season, when the wetlands gradually lose water and often completely dry. Immediately before drying, turtles move to the shallows, bury in the mud and aestivate (Kennett and Christian 1994). Pigs prey heavily on *C. rugosa* during this period, killing a large proportion of the inactive turtles (Fordham *et al.* 2006b) but possibly also prompting a density dependent response (Fordham *et al.* 2007). Although correlative analysis suggest that a fast growing, early maturing and highly fecund species like *C. rugosa* may be better equipped to compensate for relatively high levels of adult mortality (Fordham *et al.* 2007), manipulative studies are needed to confirm causation (Cappuccino & Harrison 1996).

The interaction between population growth and extrinsic and intrinstic factors, such as climatic variability and demographic structure, makes quantifying density dependence difficult (Clutton-Brock & Coulson 2002). Without replicated experimentation, it is not usually possible to separate density dependent compensation from fortuitous recovery (e.g. owing to favourable environmental conditions) following harvest mortality (Cappuccino & Harrison 1996), even in well-studied species (Pöysä *et al.* 2004). Manipulation of population size or other ecological variables such as predation pressure, provide one way to establish the presence or absence of density dependent responses (Massott 1992; Pedersen *et al.* 2004).

By manipulating density (via reduction and supplementation), we explore experimentally the demographic processes that underlie population regulation in *C. rugosa*. Specifically we test whether *C. rugosa* populations are regulated by a density dependent response in turtle survival, hatchling recruitment and subsequent survival into larger size classes, post-maturity growth and reproductive size.

Materials and methods

Study Location and Experimental Design

Seven discrete isolated billabong (waterhole) populations of *C. rugosa* were studied in central Arnhem Land, Northern Territory, Australia, from 2002 until 2006. They are referred to by their Aboriginal names. The location, regularity of drying and harvest history of six of the seven populations is described elsewhere (Fordham *et al*. 2007). The additional population, Garromgarrom: 12º18.6'S; 134º29.5'E, typically does not dry in any year and therefore is unharvested.

During January-February 2005, the densities of three populations (Imimbar, Ginmilly and Garromgarrom) were reduced and the captured animals were used to supplement the populations in Giddadella and Damdam. Reduction and supplementation involved only adult and sub-adult turtles (CL ≥ 140 mm). The numbers of turtles removed at Imimbar, Ginmilly and Garromgarrom were 142, 40 and 27 respectively. Giddadella was supplemented with 100 turtles, while Damdam was supplemented with 146. Turtles from Jibenna (12º9'S; 134º30'E) were used to cover the shortfall in supplement animals. Murrybulljuluk and Little-Giddadella were chosen as controls and were not manipulated. In 2005, turtle abundance at Little-Giddadella was reduced by an unanticipated depression in adult survival brought about by pig predation, a rare event for this waterhole (Fordham *et al*. 2007), thus we regarded Little-Giddadella as an unconstrained treatment.

The experimental design allowed key demographic parameters to be compared prior to (2003-2004) and after (2005-2006) density manipulation. Despite the formidable logistical constraints involved with manipulating remote natural systems, we were able to achieve some level of spatial and temporal control. The location of each population ensured that emigration and immigration were sufficiently low so as not to invalidate our demographic analysis (Fordham *et al.* 2007).

Trapping and Measurement Procedures

Each population was trapped twice per year, from 2002 to 2005 (Fordham *et al.* 2007). In 2005, an additional trapping session, at the beginning of the wet season, was undertaken at manipulated billabongs. In 2006 all populations were trapped from May–June (14 – 17 months after manipulation). The methodology of Fordham *et al.* (2007) was used to measure turtle size, sex turtles, estimate female reproductive activity and distinguish hatchlings, yearlings and two-year juveniles.

Survival, Density, Growth and Fecundity Analysis

Program Mark 4.2 (Colorado State University; White and Burnham 1999) was used to estimate *C. rugosa* survival (ϕ) and recapture rates (p) using live-recaptures-only models and combined live-recaptures and dead recoveries models (Burnham Models; Burnham 1993). A candidate set of survival and recapture models (2002-2006) for all populations except Garromgarrom is given elsewhere (Fordham *et al.* 2007). An identical live-recaptures-only candidate model set was created for Garromgarrom. To test the strength of evidence that manipulation influences the survival of individuals remaining at each experimental population, manipulation was treated as a factor and compared to models without this factor. Akaike's Information Criterion weights (w_i), whereby model support is scaled between 0–1 relative to all models under consideration, was used as an objective means of model comparison (Burnham and Anderson 2001).

Recapture probabilities were used to calculate population abundance and approximate 95% confidence intervals using the standard Horvitz-Thompson estimator $\{N_i = (n_i/p_i)$; Seber 1982$\}$ and following methods described by Fordham *et al.* (2007). ArcView GIS 3.2® software was used to calculate the surface area of each billabong from perimeter location points taken at the end of each wet season. Population density was calculated as number of individuals per hectare (*ha*).

Somatic growth rate was calculated as the incremental difference in carapace length divided by the number of years between captures. The *R* statistical package v2.1.1 (*R* Development Core Team 2005) was used to assess the statistical relationships between variation in post-maturity growth prior to (2003-2004) and after manipulation (2005-2006). Bootstrapping was used to estimate confidence intervals via the percentile method (Crawley 2002). A binomial generalised linear model with a log-link function was used to determine the statistical relationship between the proportion of reproducing turtles (*reproduction*) and: (i) population of origin (*site*); (ii) manipulation (yes/no; *manip*); (iii) mode of manipulation (reduced or supplemented; *manip type*); and (iv) year of capture (*yr*). The following multi-term models were also considered: *site* + *yr*, *yr* + *manip* and *yr* + *manip* + *manip type*.

Results

Survival Analysis

The most parsimonious survival model at all three reduction sites (Imimbar, Ginmilly and Garromgarrom), related survival (ϕ) and recapture rates (p) to turtle size (Table 6.1; see Appendix Table 6.3 for entire model set). Adding density reduction as a factor at Imimbar resulted in a slightly lower model ranking. There was no support for a model that related ϕ and p to reduction alone (Table 6.1). There was little support for modelling density reduction as an additive or sole reduction term at Ginmilly or Garromgarrom (Table 6.1). Therefore, density reduction had little influence on *C. rugosa* survival.

According to the most parsimonious survival model for Giddadella, severity of pig rooting had the largest influence on ϕ and p, while r was influenced by the presence or absence of water and turtle size (Table 6.1). Adding density supplementation as a factor at Giddadella resulted in a lower model ranking, but not substantially so. There was little support for a model that related ϕ and p to supplementation alone (Table 6.1). The best supported survival model for the second supplementation site, Damdam, related ϕ, p and r to the presence or absence of water, while turtle size positively influenced r. Models that treated supplementation as an additive or sole reduction term performed substantially

Table 6.1: Summary set of mark-recapture models, showing Akaike's Information Criterion (AIC_c), number of parameters (k), deviance (Dev), change in AIC_c compared to the best-ranked model (ΔAIC_c) and model weights (w_i), for density reduction and supplement populations. Turtle size (*s*) was modelled as a covariate. The density reduction (*red*) and supplementation (*sup*) were treated as cofactors, as were the presence or absence of water (*wtr*) and severity of pig rooting (*rt*). Where necessary, a relative index of trapping period (*t*) averaged across all individuals in the population was modelled as an across population covariate. See Appendix Table 6.3 for the complete model set**.**

Site	Treatment	Model	AIC_c	*k*	Dev	ΔAIC_c	w_i
Imimbar	*Reduced*	$\phi (s)p(s^{+} t)$	729.45	5	719.25	0.00	0.50
		$\phi (s^{+} red)p(s^{+} red^{+} t)$	731.24	7	716.87	1.79	0.21
		$\phi (red)p(red^{+} t)$	739.831	5	729.64	10.38	0.00
Ginmilly	*Reduced*	$\phi (s)p(s^{+} t)$	226.82	5	216.10	0.00	0.68
		$\phi (s^{+} red)p(s^{+} red^{+} t)$	230.77	7	215.39	3.94	0.09
		$\phi (red)p(red^{+} t)$	238.53	5	227.81	11.71	0.00
Garromgarrom	*Reduced*	$\phi (s)p(s^{+} t)$	250.06	5	239.44	0.00	0.42
		$\phi (s^{+} red)p(s^{+} red^{+} t)$	254.78	7	239.58	4.71	0.04
		$\phi (red)p(red^{+} t)$	256.46	5	245.83	6.39	0.02
Giddadella	*Supplement*	$\phi (rt)p(rt^{+} t)r(wrt^{+} s)f(1)$	900.82	9	882.38	0.00	0.34
		$\phi (rt^{+} sup)p(rt^{+} sup^{+} t)r(wrt^{+} s)f(1)$	901.99	11	879.34	1.17	0.19
		$\phi (sup)p(sup^{+} t)r(wrt^{+} s)f(1)$	908.58	9	890.14	7.76	0.01
Damdam	*Supplement*	$\phi (wrt)p(wrt)r(wrt^{+} s)f(1)$	498.95	8	482.44	0.00	0.37
		$\phi (wrt^{+} sup)p(wrt^{+} sup)r(wrt^{+} s)f(1)$	502.24	10	481.46	3.29	0.07
		$\phi (sup)p(sup)r(wrt^{+} s)f(1)$	503.29	8	486.78	4.33	0.04

worse (Table 6.1). Therefore, density supplementation also had little influence on *C. rugosa* survival.

Recruitment

Population growth responded positively to a substantial reduction in turtle density (> 50%) at Imimbar, Ginmilly and Garromgarrom (Table 6.2). Increased juvenile numbers (CL < 140 mm) at all reduction sites in 2006 (post manipulation; Table 6.2) resulted in a marked increase in the proportion of yearlings (Figure 6.1), suggesting that a negative perturbation in density is immediately compensated by increased hatchling recruitment.

Juvenile abundance did not show a negative response to supplementation (> 50% increase in density), which is surprising given the strong positive response to density reduction (Table 6.2). Population abundance at Damdam declined following supplementation but juvenile numbers remained relatively unchanged (Table 6.2). This signified that the decline in abundance was not a symptom of reduced juvenile recruitment. The number of juveniles at Giddadella increased substantially following supplementation, owing heavily to a proportional increase in hatchling recruits (Figure 6.1), causing a concomitant boost to population size (Table 6.2).

Turtle density at the experimental control, Murrybulljuluk, did not vary significantly between 2004 and 2006; juvenile numbers remained constant (Table 6.1), though their age class differed (Figure 6.1). At Little-Giddadella (unconstrained treatment) juveniles were rare in 2004, but increased in 2006 owing to increased hatchling recruitment (Figure 6.1). Population density did not change over this period (Table 6.1).

Maturity and Reproduction

A downward shift in density failed to positively influence the proportion of small, reproductively active females (CL = 180-200 mm; Appendix Figure 6.2). Small female turtles were rarely gravid during the peak of the breeding season at Imimbar prior to and after reduction [(16% (*n* = 12); 28% (*n* = 7)]. At Ginmilly and Garromgarrom, all turtles with carapace lengths < 220 mm (*n* = 12 and *n* = 8) were not gravid, regardless of density.

Table 6.2: Total population size, turtle density, juvenile population size (carapace length <140 mm) and female annual post-maturity growth (CL >220 mm) at manipulated and control populations, prior to manipulation (2004), directly after experimental manipulation (2005), and 14 - 17 months later (2006). Numbers in parentheses are 95% confidence intervals. [Note : Pre-manipulation density at Giddadella and Damdam was estimated at the beginning of 2005, prior to supplementation, owing to a strong negative shift in survival towards the end of 2004 (see Methods)]

Population	Treatment	Year	Total Population Size	Turtle Density (n/ha)	Juvenile Population Size	Mature Female Growth (mm)
Imimbar	*Reduced*	2004	243 (201-307)	10.4 (8.6-13.2)	7 (6-9)	0.52 (0.14-0.99)
		2005	101 (59-165)	4.4 (2.6-7.2)		
		2006	174 (128-272)	8.1 (6.0-12.7)	47 (35-74)	1.49 (0.65-2.35)
Ginmilly	*Reduced*	2004	59 (44-87)	4.4 (3.3-6.5)	0	0.82 (0.39-2.35)
		2005	19 (4-47)	1.6 (0.3-3.9)		
		2006	58 (41-98)	4.9 (3.4-8.2)	17 (12-29)	1.57 (0.49-2.89)
Garromgarrom	*Reduced*	2004	42 (34-53)	4.5 (3.6-5.7)	8 (7-11)	0.82 (0.39-1.29)
		2005	15 (7-26)	1.7 (0.8-3.0)		
		2006	38 (30-49)	4.4 (3.5-5.7)	15 (12-20)	0.44 (0.00-1.32)
Giddadella	*Supplemented*	2005*	99 (81-129)	3.1 (2.5-4.0)	37 (30-48)	4.85 (3.64-6.19)
		2005	199 (181-229)	6.4 (5.8-7.4)		
		2006	324 (223-668)	7.9 (5.4-16.3)	160 (104-350)	2.92 (0.83-4.73)
Damdam	*Supplemented*	2005*	180 (116-405)	3.0 (2.0-6.9)	36 (23-81)	11.07 (9.89-12.44)
		2005	326 (262-551)	7.6 (6.1-12.9)		
		2006	220 (151-488)	3.6 (2.5-8.0)	37 (23-89)	2.27 (0.79-4.11)
Murrybulljuluk	*Control*	2004	179 (121-345)	2.6 (1.7-5.0)	62 (42-119)	3.04 (2.23-3.80)
		2006	183 (117-417)	3.1 (2.0-7.1)	61 (39-139)	3.06 (2.14-3.98)
Little-Giddaddella	*Unconstrained Treatment*	2004	32 (28-40)	8.3 (7.2-10.3)	2 (1-2)	1.06 (0.24-1.94)
		2006	35 (30-43)	8.8 (7.5-10.8)	7 (6-8)	1.57 (0.20-3.37)

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* Prior to supplementation

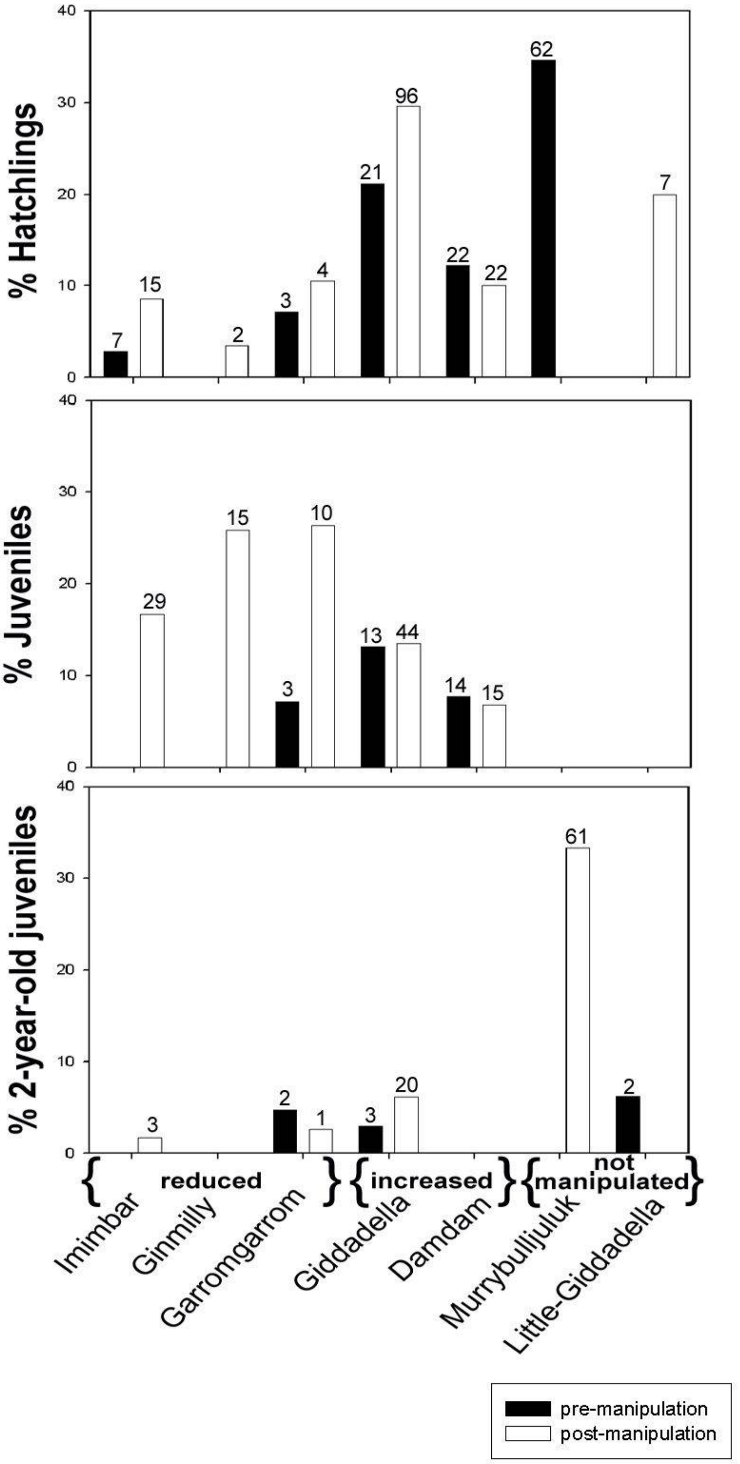


Figure 6.1: Percentage of total population size represented by (**a**) hatchlings, (**b**) yearlings and (**c**) 2-year-old juveniles, prior to and following population manipulation of snake-necked turtles at seven sites in northern Australia. The experimental treatments were density reduction (Imimbar, Ginmilly and Garromgarrom), supplementation (Giddadella and Damdam), an unmanipulated control (Murrybulljuluk) and an unconstrained treatment (Little-Gidddadella; see Methods). Numbers above bars represent estimated number of individuals.

In contrast, large female turtles (CL ≥ 220 mm) tended to be gravid prior to and after density reduction at Imimbar [53% (*n* = 47); 69% (*n* = 16)] Ginmilly [76% (*n* = 25); 83% (*n*=18)] and Garromgarrom [76% (*n* = 17); 88% (*n* = 7)]. Moreover, increasing density did not cause a decline in the proportion of small reproductively active turtles at Giddadella. Female turtles < 200 mm tended to be gravid prior to and after supplementation [60% (*n* = 15); 80% (*n* = 5)]. The reproductive activity of large [62% (*n* = 26); 33% (*n* = 6)] as well as small [83% (*n* = 6); 17% (*n* = 6)] females declined after supplementation at Damdam (Appendix Figure 6.2).

Reproductive activity in large females (CL > 220 mm) was not influenced by manipulation. The null was the best-ranked model ($w_i = 0.724$), with relatively little support for the models *reproduction = yr* ($\Delta_i = 2.31$; $w_i = 0.227$) and *reproduction = yr + manip* ($\Delta_i = 5.41$; $w_i = 0.043$). There was essentially no support for any of the other models ($w_i < 0.001$; see Methods).

Post-maturity Growth

Annual somatic growth of large females (CL > 220 mm) was unaffected by population reduction at Imimbar, Ginmilly and Garromgarrom (Table 6.1). Growth declined significantly in response to supplementation at Damdam [11.07 mm yr^{-1} (CI = 9.89-12.44); 2.27 mm yr^{-1} (CI = 0.79-4.11)]. Growth declined with supplementation at Giddadella but the response was not pronounced [4.85 mm yr^{-1} (CI = 3.64-6.19); 2.92 mm yr^{-1} (CI = 0.83-4.73)]. Growth remained constant at Murrybulljuluk (control) and Little-Giddadella (unconstrained) over the same period (Table 6.1).

Discussion

Although freshwater turtles are heavily exploited for human consumption (Gibbons *et al.* 2000), the prevailing view is that freshwater turtles do not display density-dependent responses and so harvesting sub-adult and adult turtles at almost any level is inherently unsustainable and therefore unacceptable (Congdon *et al.* 1993 & 1994; Cunnington & Brooks 1996; Heppell 1998). Yet *Chelodina rugosa* have persisted over a long period of subsistence exploitation in tropical northern Australia (Fordham *et al.* 2006b). Through spatially replicated manipulation of population density, we show that hatchling recruitment and their survival into larger size classes provides resilience to negative perturbations in adult and sub-adult abundance. This suggests that density dependent compensation is at least partially responsible for population persistence in *C. rugosa* over the long period of interaction with people and more recently introduced pigs.

Population growth in *C. rugosa* responds positively to density reduction mainly via increased juvenile recruitment rather than compensations in survival. Remarkably, at some populations, turtle density took less than two years to spring back to a pre-manipulation size (Table 6.1). Traits that contribute heavily to population growth in long-lived vertebrates, such as adult survival, tend to be buffered against changes in population density (Pfister 1998). Conversely, traits such as hatchling /newborn survival contribute proportionately less to population growth, but are more responsive to changes in population density (Gaillard *et al.* 1998). Similarly, we show that hatchling survival in *C. rugosa* is more responsive to fluctuations in density than sub-adult and adult survival. Our population manipulations coincided with the onset of the wet season, when hatchlings emerge from the nest (Fordham *et al.* 2006a). A large number of yearlings were recorded 14 – 17 months after the downward displacement in population size, indicating that density reductions were compensated swiftly by increased hatchling recruitment (Figure 6.1). We can be confident that the interaction between low density and increased hatchling recruitment was not driven by high per capita resource availability during reproduction, because the recruits of 2005 hatched from eggs laid prior to manipulation. Instead, recovery was likely facilitated by decreased resource competition or a reduction in cannibalism. Empirical evidence from long-term and manipulative studies of fish supports this hypothesis (Rose *et al.* 2001).

Juvenile numbers remained unchanged between 2004-2006 in the control population at Murrybulljuluk (Table 6.1). High hatchling recruitment at this billabong in 2004 was probably a compensatory response to a rare negative perturbation in sub-adult and adult abundance (Fordham *et al.* 2007), which produced a large number of two year-olds in 2006 (Figure 6.1). Juvenile recruitment increased at Little-Giddadella (unconstrained treatment) in 2006 (Table 6.1), which we regard as an anomaly. Pig predation caused a rare periodic depression in adult survival at Little-Giddadella in 2005 (Fordham *et al* 2007), reducing turtle density and triggering rapid hatchling recruitment (Figure 6.1). This finding is also consistent with the *a priori* hypothesis that *C. rugosa* populations are regulated by density.

Population size declined following an artificial increase in density at only one of two supplemented populations. One year after supplementation, population density at Damdam declined to a density, reasonably similar to that recorded prior to manipulation (Table 6.1). However, density independent processes were primarily to blame. Towards the end of 2005 (8-10 months after supplementation), pigs preyed heavily on supplemented and native turtles (Fordham *et al*. 2007) causing a downward shift in abundance, which likely inhibited any direct density dependent response. High turtle density at the beginning of 2005 at Damdam (Table 6.1) also negatively influenced female reproductive activity in 2005 and 2006 (Appendix Figure 6.2), reducing the potential number of hatchling recruits.

Population growth at Giddadella surprisingly continued to increase subsequent to supplementation (Table 6.1). We conjecture that turtle density at Giddadella at the beginning of 2005 was probably well below carrying capacity due to pig predation in 2004 (Fordham *et al*. 2007). At a supplemented density of 6.4 turtles/ha, sufficient resources remained available to support an ongoing high level of reproductive activity amongst native (Appendix Figure 6.2) and supplemented turtles, encouraging increased hatchling recruitment in 2006 (Figure 6.1). A rare flooding event at Giddadella in 2006 reduced turtle density, promoting juvenile survival; and permitted a rare episode of turtle immigration (Fordham unpublished data). In conjunction with increased number of potential hatchlings, these factors probably contributed to Giddadella's growth in 2006.

Small gravid turtles (CL < 200 mm) are common in *C. rugosa* populations where survival is periodically low, yet rare in populations where survival is consistently high (Fordham *et al*. 2007). A shift in size of maturity towards earlier ontogenetic stages can promote persistence in response to low adult survival (Abrams & Rowe 1996). Small gravid female turtles were rare or absent prior to, and after, density reduction at Imimbar, Ginmilly and Garromgarrom (relatively high survival) but remained common after supplementation at Giddadella (relatively low survival; Appendix Figure 6.2). Thus, decreased size of maturity in *C. rugosa*, as in other reptiles (Bronikowski and Arnold 1999), and fish (Olsen *et al*. 2004), is probably a local adaptation – an evolved response that promotes demographic resilience under conditions of comparatively low survival.

Food availability positively influences somatic growth in sea turtles (Bjorndal *et al*. 2000), providing an important conduit for population growth and thus resilience to density perturbations (Barlow 1992). Prior to supplementation, post-maturity growth was rapid at Damdam and Giddadella, leading to an increase in age-specific fecundity in response to low survival (Fordham *et al*. 2007). Increasing sub-adult and adult density at Damdam induced a significant negative somatic growth response. At Giddadella the negative growth response was not as pronounced (Table 6.1). Post-maturity growth was unaffected by population reduction. This is not unexpected, because density dependent processes often respond nonlinearly (Coulson *et al*. 2001). It may be that populations of *C. rugosa* need to be held at densities well below carrying capacity, or experience an extended period of reduced density, before a positive shift in post-maturity growth is manifested.

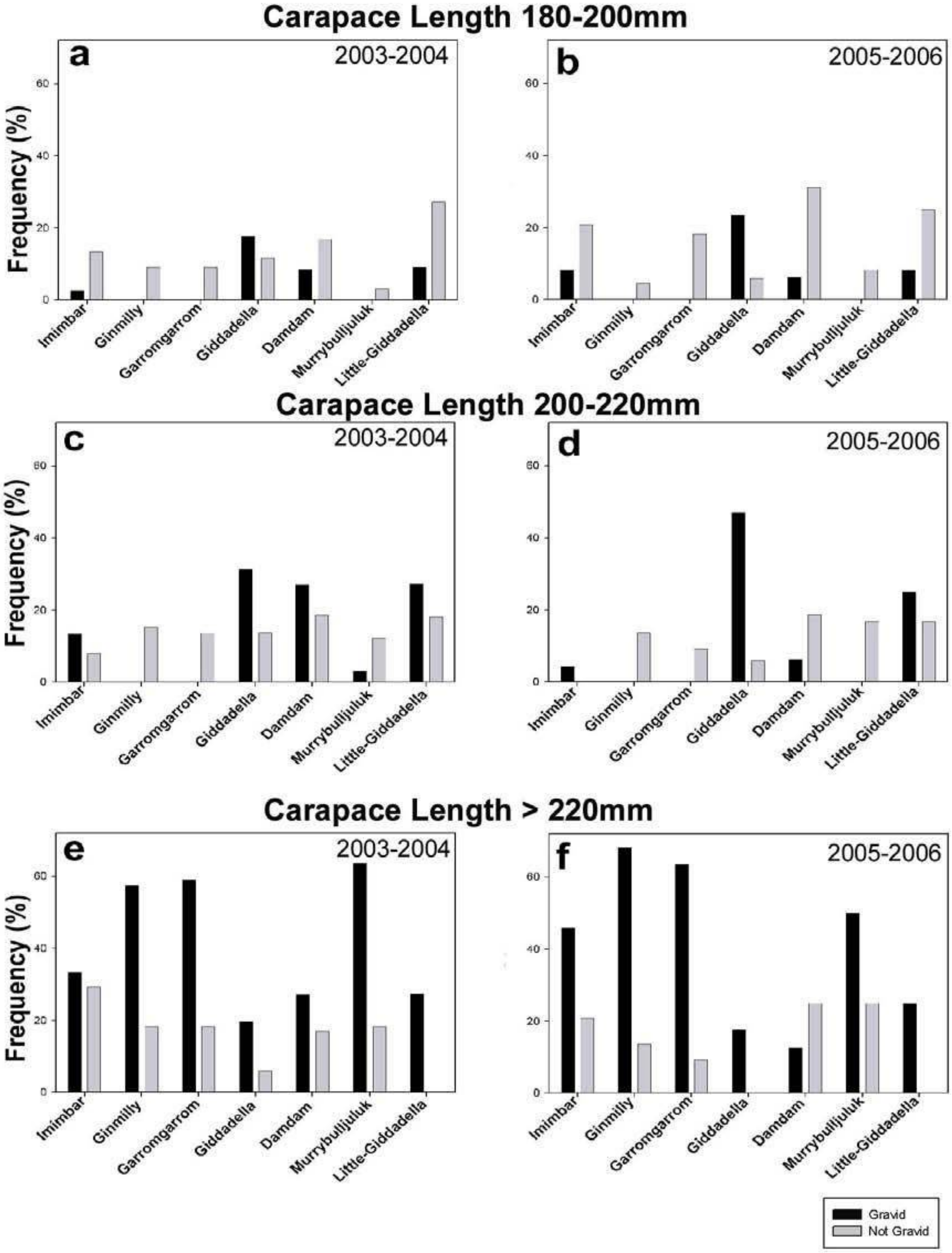
Our manipulative experiments demonstrate that sub-adult and adult losses in freshwater turtles can be replaced quickly via increased hatchling recruitment and their survival into large size classes. This density-dependent response promotes resilience to high levels of harvest and pig predation. This finding challenges the general perception that high sub-adult and adult survival is crucial for achieving long-term population stability in freshwater turtles (Congdon *et al*. 1993 & 1994; Cunnington & Brooks 1996; Heppell 1998). We posit that the sustainability, or otherwise, of turtle harvesting should be assessed at a species level, arguing against a universal generalisation that freshwater turtles are inevitably vulnerable to off-take. The harvest of turtles with ‘slow’ life histories may warrant caution, but equally so, species with ‘fast’ life histories, similar to *C. rugosa*, may afford a level of sub-adult and adult harvest, owing to a compensatory increase in hatchling recruitment.

Appendices

Appendix Table 6.3: Entire mark-recapture model set showing Akaike's Information Criterion (AIC_c), number of parameters (k), deviance (Dev), change in AIC_c compared to the best-ranked model (ΔAIC_c) and model weights (w_i), for density reduced and supplement populations. Juvenile turtles (size < 140 mm) and adult and sub-adult turtles (size ≥140 mm) were grouped and treated as a grouped factor (*g*). Turtle size (*s*) was modelled as a covariate. Density reduction (*red*) and supplementation (*sup*) were treated as cofactors, as was the presence or absence of water (*wtr*), harvest (*h*) and monsoonal rains (*mr*) and the severity of pig rooting (*rt*). Where necessary, a relative index of trapping period (*t*) averaged across all individuals in the population was modelled as an across population covariate.

Site	Treatment	Model	AIC_c	k	Dev	ΔAIC_c	w_i
Imimbar	*Reduction*	**$\phi(s)p(s^{+}t)$**	729.446	5	719.251	**0.000**	**0.509**
		$\phi(mr^{+}s)p(mr^{+}s^{+}t)$	730.989	7	716.621	1.543	0.235
		$\phi(s^{+}red)p(s^{+}red^{+}t)$	731.236	7	716.869	**1.790**	**0.208**
		$\phi(mr)p(mr^{+}t)$	735.767	5	725.571	6.321	0.022
		$\phi(.)p(t)$	735.945	3	729.868	6.499	0.020
		$\phi(g)p(g^{+}t)$	739.191	6	726.917	9.745	0.004
		$\phi(red)p(red^{+}t)$	739.831	5	729.636	**10.385**	**0.003**
Ginmilly	*Reduction*	**$\phi(s)p(s^{+}t)$**	226.825	5	216.102	**0.000**	**0.676**
		$\phi(mr^{+}s)p(mr^{+}s^{+}t)$	229.052	7	213.669	2.228	0.222
		$\phi(s^{+}red)p(s^{+}red^{+}t)$	230.768	7	215.385	**3.944**	**0.094**
		$\phi(.)p(t)$	237.114	3	230.831	10.289	0.004
		$\phi(red)p(red^{+}t)$	238.531	5	227.808	**11.706**	**0.002**
		$\phi(mr)p(mr^{+}t)$	239.996	5	229.273	13.172	0.001
		$\phi(g)p(g^{+}t)$	242.777	6	229.753	15.952	0.000
Garromgarrom	*Reduction*	**$\phi(s)p(s^{+}t)$**	250.063	5	216.102	**0.000**	**0.419**
		$\phi(g)p(g^{+}t)$	250.554	6	213.669	0.490	0.328
		$\phi(.)p(t)$	252.508	3	215.385	2.445	0.123
		$\phi(mr^{+}s)p(mr^{+}s^{+}t)$	254.238	7	230.831	4.174	0.052
		$\phi(s^{+}red)p(s^{+}red^{+}t)$	254.776	7	227.808	**4.713**	**0.040**
		$\phi(mr)p(mr^{+}t)$	256.018	5	229.273	5.955	0.021
		$\phi(red)p(red^{+}t)$	256.457	5	229.753	**6.393**	**0.017**

Giddadella	*Supplement*	***ϕ (rt)p(rt + t)r(wtr + s)f(1)***	900.820	9	882.377	**0.000**	**0.337**
		ϕ (rt + sup)p(rt + sup + t)r(wtr + s)f(1)	901.993	11	879.341	**1.173**	**0.187**
		ϕ (rt + s)p(rt + s + t)r(wtr + s)f(1)	902.503	11	879.851	1.683	0.145
		ϕ (wtr)p(wtr + t)r(wtr + s)f(1)	903.095	9	884.653	2.275	0.108
		ϕ (rt)p(rt + t)r(wtr)f(1)	903.421	8	887.068	2.601	0.092
		ϕ (rt+s)p(rt + s + t)r(wtr)f(1)	905.441	10	884.899	4.621	0.033
		ϕ (wtr)p(wtr + t)r(wtr)f(1)	905.665	8	889.312	4.845	0.030
		ϕ (wtr + s)p(wtr + s + t)r(wtr + s)f(1)	905.991	11	883.339	5.171	0.025
		ϕ (rt + g)p(rt + g + t)r(wtr + s)f(1)	906.206	14	877.161	5.386	0.023
		ϕ (sup)p(sup + t)r(wtr + s)f(1)	908.578	9	890.136	**7.758**	**0.007**
		ϕ (wtr + s)p(wtr + s + t)r(wtr)f(1)	909.102	10	888.560	8.282	0.005
		ϕ (wtr + g)p(wtr + g + t)r(wtr + s)f(1)	909.485	14	880.440	8.666	0.004
		ϕ (rt + g)p(rt + g + t)r(wtr)f(1)	910.968	13	884.065	10.148	0.002
		ϕ (wtr + g)p(wtr + g + t)r(wtr)f(1)	911.584	13	884.681	10.765	0.002
		ϕ (s)p(s)r(s)f(1)	963.996	7	949.722	63.176	0.000
		ϕ (.)p(.)r(.)f(1)	964.597	4	956.500	63.780	0.000
Damdam	*Supplement*	***ϕ (wtr)p(wtr)r(wtr + s)f(1)***	498.952	8	482.441	**0.000**	**0.366**
		ϕ (wtr + g)p(wtr + g)r(wtr + s)f(1)	500.197	12	475.075	1.245	0.197
		ϕ (wtr)p(wtr)r(wtr)f(1)	500.796	7	486.400	1.844	0.146
		ϕ (wtr + sup)p(wtr + sup)r(wtr + s)f(1)	502.244	10	481.459	**3.292**	0.071
		ϕ (wtr + g)p(wtr + g)r(wtr)f(1)	502.913	11	479.967	3.961	0.051
		ϕ (wtr + s)p(wtr + s)r(wtr + s)f(1)	503.224	10	482.438	4.272	0.043
		ϕ(h)p(h)r(wtr + s)f(1)	503.233	8	486.722	4.281	0.043
		ϕ (sup)p(sup)r(wtr + s)f(1)	503.286	8	486.776	**4.334**	0.042
		ϕ (wtr + s)p(wtr + s)r(wtr)f(1)	505.027	9	486.387	6.075	0.018
		ϕ (h + s)p(h + s)r(wtr + s)f(1)	505.943	10	485.157	6.991	0.011
		ϕ (h + s)p(h + s)r(wtr)f(1)	507.838	9	489.197	8.886	0.004
		ϕ (h + g)p(h + g)r(wtr + s)f(1)	507.889	12	482.767	8.937	0.004
		ϕ (h)p(h)r(wtr)f(1)	507.945	7	493.549	8.992	0.004
		ϕ (h + g)p(h + g)r(wtr)f(1)	511.379	11	488.433	12.427	0.001
		ϕ (.)p(.)r(.)f(1)	537.3272	4	529.187	38.3751	0.000
		ϕ (s)p(s)r(s)f(1)	537.5717	7	523.176	38.6196	0.000



Appendix Figure 6.2: Reproductive status of female snake-necked turtles during 2003-2004 (**a**, **c** and **e**) and 2005-2006 (**b**, **d** and **f**) at reduced (Imimbar, Ginmilly and Garromgarrom), supplemented (Giddadella and Damdam), control (Murrybulljuluk) and unconstrained treatments (Little-Gidddadella). Frequency is the cumulative frequency of total female turtles caught during peak-breeding season (see Methods).

Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: managing a tropical freshwater turtle for sustainability and conservation

Picture: Talvin Brown [M. Hatt]

Fordham, D., Georges, A. & Brook, B. W. (2007) Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: managing a tropical freshwater turtle for sustainability and conservation. *Journal of Applied Ecology,* in review.

Summary

Until recently, the northern snake-necked turtle (*Chelodina rugosa*; Ogilby 1890) provided a seasonal source of protein for indigenous communities in tropical northern Australia. Today, feral pigs (*Sus scrofa*; Linnaeus 1758) exert a heavy and unrelenting predation pressure on *C. rugosa*, compromising subsistence harvest rates and threatening local persistence. We investigate the impacts of pig predation and harvest (subsistence and commercial) on *C. rugosa* persistence at discrete water holes using a stage-based matrix population model. Vital rates varied with wet season rainfall, pig predation and harvest. In addition, hatchling survival was density dependent. We show that even moderate estimates of pig-related turtle mortality exceed levels that can be offset by increased hatchling survival, leading to rapid population decline and certain elimination of affected populations within 30 years. Conversely, in the absence of pigs, compensatory increases in hatchling survival were sufficient to allow an annual harvest of up to 20% of sub-adult and adult *C. rugosa* without causing extirpation or substantial population suppression.

Synthesis and Application

Our modelling shows that periodic local culling of pigs, fencing of wetlands to exclude predators and hatchling supplementation to off-set losses to predation are all viable management strategies to ensure an ongoing subsistence harvest. These findings are broadly relevant to applied ecology, because they challenge the prevailing view that it is not possible to harvest long-lived turtles in a sustainable way.

Introduction

Density dependence is a pervasive feature of the population dynamics of most species (Brook & Bradshaw 2006), allowing populations to sustain some level of harvest without threatening persistence (Boyce, Sinclair & White 1999; Rose *et al.* 2001). Some long-lived vertebrates have persisted under many millennia of traditional harvesting, albeit with a reduction in population size (Frazer 2003; Pandolfi *et al.* 2003). However, the additional effects of contemporary human impacts, such as habitat destruction, commercial harvesting, invasive species and climate change (Tynan & DeMaster 1997; Wilcove *et al.* 1998; Jackson *et al.* 2001; Sodhi & Brook 2006), place once-sustainable harvest regimes in potential jeopardy (Marsh 1996; Derocher, Lunn & Stirling 2004; Hunter & Caswell 2005). To prevent unacceptable levels of future population decline in the face of these new challenges, subsistence harvest rates will often need adjustment to suit contemporary environmental conditions (Heinsohn *et al.* 2004).

The sustainability of harvest (whether harvesting allows for stable population sizes over the long term) depends on the timing and selectivity of the harvest (Jensen 2000; Freckleton *et al.* 2003), the life history strategy of the organism (Heppell, Caswell & Crowder 2000; Musick *et al.* 2000) and the level of additional human-imposed mortality (Hunter & Caswell 2005). Chelonians (turtles and tortoises) have a life history strategy characterised by low egg and hatchling survival, delayed maturity and high juvenile, sub-adult and adult survival (Heppell 1998; Chaloupka & Limpus 2002). Thus population growth is most sensitive to variation in sub-adult and adult survival (Doak, Kareiva & Klepetka 1994; Cunnington & Brooks 1996; Heppell *et al.* 1996b) and fertility, a parameter that combines fecundity and adult survival (Chaloupka 2002). Harvests of freshwater turtles are often biased towards larger, older animals (Close & Siegel 1997; Fordham *et al.* 2006b; Georges, Guarino & Bito 2006a). This can pose a threat to population persistence, because these individuals have a high reproductive value (Congdon, Dunham & van Loben Sels 1993, 1994). Although high rates of adult survival are certainly crucial for some turtle species, the generality of this statement has recently been challenged (Fordham, Georges & Brook 2007a,b). Long-lived organisms display a differential vulnerability to exploitation; fast growing, early maturing and highly fecund species, that nevertheless also breed for many years once reaching maturity, may be equipped to quickly respond to some level of adult harvest mortality (Walker 1998; Stevens *et al.* 2000).

Population models provide useful tools for integrating information on a species' ecology and life history to assess the impact of harvest and explore the relative benefit of alternative management actions (Milner-Gulland *et al.* 2001; Brook & Whitehead 2005a,b; Taylor *et al.* 2005). Deterministic and stochastic matrix models have been widely used to assess the sustainability of turtle harvesting and other human disturbances (Crouse, Crowder & Caswell 1987; Heppell, Crowder & Crouse 1996a; Heppell *et al.* 1996b; Chaloupka 2002; Spencer & Thompson 2005). To date, population models incorporating density dependence in vital rates have been regarded as unnecessary for chelonians (e.g., Doak *et al.* 1994; Chaloupka 2002), although there are some exceptions (Chaloupka 2004; Tiwari *et al.* 2006). The interaction between hatchling/newborn recruitment and density is critical for population regulation in many long-lived vertebrates (Fowler 1987; Gaillard, Festa-Bianchet & Yoccoz 1998), including turtles (Tiwari *et al.* 2006; Fordham *et al.* 2007a,b), and should be considered in any realistic harvest model.

Freshwater turtles have survived a long period of interaction with people in tropical northern Australia owing, in part, to density dependent compensatory strategies (Fordham *et al.* 2007a,b). Until recently, aestivating northern snake-necked turtles (*Chelodina rugosa*; Ogilby 1890) provided a seasonal source of protein for indigenous communities living on, or near, ephemeral wetlands (Russell-Smith *et al.* 1997). Today feral pigs (*Sus scrofa*; Linnaeus 1758), an exotic predator, prey heavily on *C. rugosa* providing an unrelenting predation pressure, compromising subsistence harvest rates and threatening local persistence (Fordham *et al.* 2006b).

In this study we investigate the impacts of pig predation and harvest (subsistence and commercial [largely for the pet trade]) on *C. rugosa* persistence at discrete water holes in northern tropical Australia, and compare the performance of competing management strategies. We develop a pre-breeding stage-based matrix population projection (Caswell 2001), with hatchling survival modelled as a density dependent function. Reproduction and mortality in the matrix varied stochastically with wet season rainfall, pig predation and harvest. The broader goal of this work is to test the validity of the commonly held view that sub-adult and adult turtle harvests, at almost any level, are unsustainable (Congdon *et al.* 1993, 1994; Cunnington & Brooks 1996; Heppell 1998).

Materials and methods

Ecological System

Chelodina rugosa attains high densities in the ephemeral swamps and other wetlands of tropical northern Australia (Cogger 2000) and the Fly Delta of New Guinea (Georges *et al.* 2006a) [Figure 7.1a]. Turtle activity is punctuated each year by the dry season, when the wetlands recede and often completely dry. Immediately before drying, turtles move to the shallows, bury in the mud and aestivate (Kennett & Christian 1994). At sites where pig abundance is high, pigs prey heavily on turtles, reducing survival during the weeks prior to drying (Fordham *et al.* 2006b). At sites of low pig abundance, subsistence harvesting reduces the survival of aestivating turtles (Fordham *et al.* 2007a). Reproduction coincides with the wet season, when wetlands refill and food availability is high (Fordham, Georges & Corey 2006a). Rainfall in the wet-dry tropics is highly variable, both within and across years, in the quantity that falls and its timing (Taylor & Tulloch 1985) [Figure 7.1b]. In unusually wet years wetlands do not dry, turtles do not aestivate, harvesting and pig predation is limited and thus turtle survival remains high (Fordham *et al.* 2007a).

Today, indigenous communities are eager to utilise wildlife both commercially and for subsistence (Altman & Cochrane 2005). A local indigenous industry has recently been established producing *C. rugosa* hatchlings for the domestic pet turtle market with a view to expanding to harvesting sub-adult and adult turtles (Fordham, Georges & Corey 2007d).

Model Structure

We used stage and sex-structured matrix models to explore the impact of harvesting and pig predation on *C. rugosa*. Stage-structured matrices are commonly used to model turtle population growth because chelonians are often difficult to age, and display distinct life history traits such as sexual dimorphism and size dependent maturity and survival (Doak *et al.* 1994; Cunnington & Brooks 1996; Heppell *et al.* 1996a,b). The transition probabilities of stage based models incorporate the probability of making a transition from one stage to the next between times i and $i + 1$, conditional on surviving (Nichols *et al.* 1992). The probability of surviving and remaining in the same stage (P) and the probability of surviving and moving into the next stage (G) were calculated for stages one to six using the equations:

Fig. 7.1a

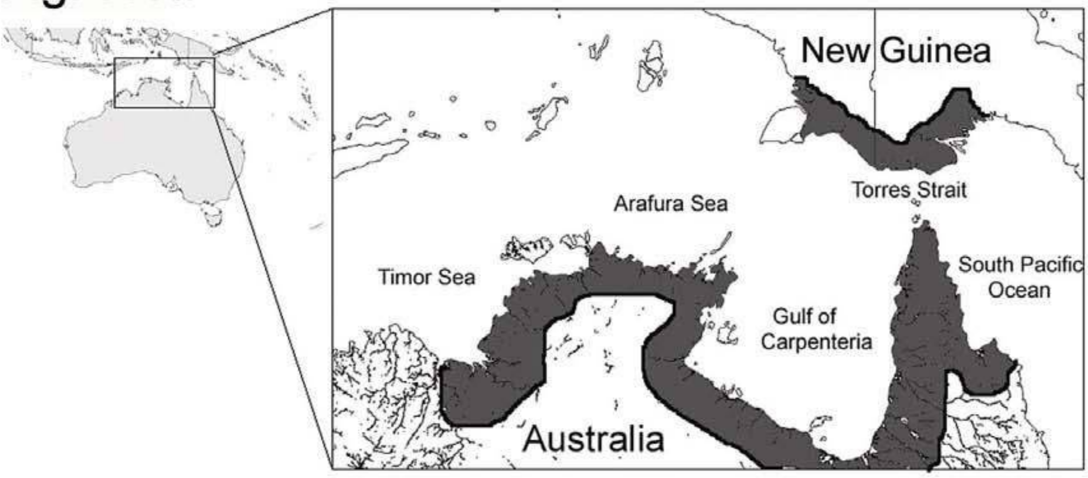


Fig. 7.1b

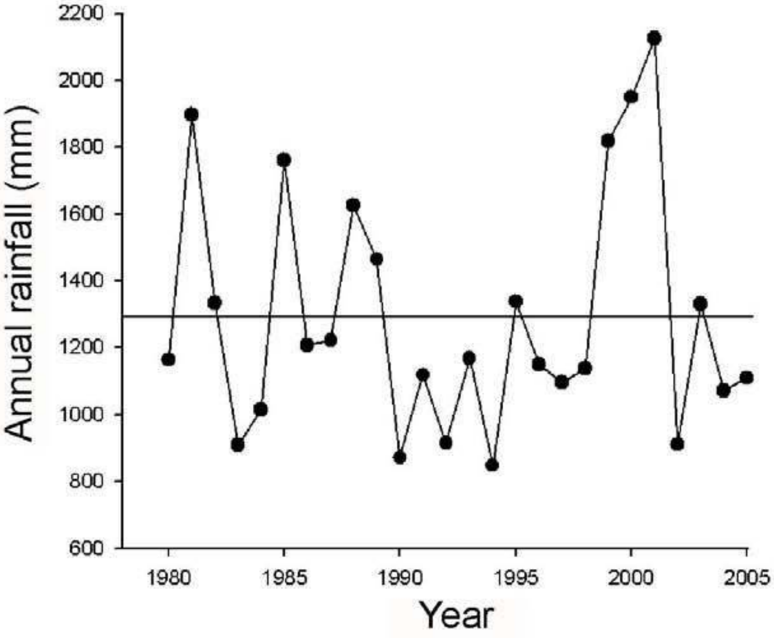


Figure 7.1: Distribution of *Chelodina rugosa* [Fig. 7.1a] and annual rainfall in the Maningrida region 1980-2005 (Australian Bureau of Meteorology unpublished data) [Fig. 7.1b]. Horizontal line shows mean annual rainfall (1290 mm).

$$\mathrm{P} = \left(\frac{1-\Phi_i^{\,di-1}}{1-\Phi_i^{\,di}} \right) \Phi_i \tag{1}$$

$$\mathrm{G} = \frac{\Phi^{di}(1-\Phi)}{1-\Phi^{di}} \tag{2}$$

where Φ is survival and d_i is the number of years between stages (Crouse *et al.* 1987).

The matrix model consisted of four female stages and two male stages. Stage one (S_1) and five (S_5) represented yearlings and two-year-old juvenile females and males (carapace length [CL] < 140 mm); stage two (S_2), sub-adult females (CL = 140-180 mm); stage three (S_3), small adult females (CL ≥ 180-220 mm); stage four (S_4), large adult females (CL ≥ 220 mm); and stage six (S_6) represented mature males (CL ≥ 140 mm). Reproductive stages each have a fecundity rate (*F*). Egg mortality and hatchling survival (0 year-olds) were included in the fecundity parameter. The transition matrix **A** describing the flux of individuals from one year to the next took the form:

$$\mathrm{A} = \begin{pmatrix} P_1 & 0 & F_3 & F_4 & 0 & 0 \\ G_1 & P_2 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_5 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 \end{pmatrix}$$

Demographic Parameters

We assumed that emigration and immigration were minimal, owing to (i) choice of study sites (discrete, isolated billabongs; Fordham *et al.* 2007a) and (ii) *C. rugosa* tend to aestivate rather than disperse in response to the periodic absence of water (Fordham *et al.* 2006b). The impact of drying, pig predation and harvest on survival (S_1-S_6) were based on detailed capture-mark-recapture studies (Fordham *et al.* 2006b; Fordham *et al.* 2007a; see Table 7.1). Growth in *C. rugosa* is sexually dimorphic; males approach asymptotic size

Table 7.1: Cormack-Jolly-Seber and live-recapture and dead recovery survival estimates for *Chelodina rugosa* under different subsistence harvest and predation scenarios (after Fordham *et al.* 2006b, 2007a). S_1 and S_5 represent yearlings and two-year-old juvenile females and males (carapace length CL < 140 mm); S_2, sub-adult females (CL = 140-180 mm); S_3, small adult females (CL ≥ 180-220 mm); S_4, large adult females (CL ≥ 220 mm); and S_6 represents mature males (CL ≥ 140 mm). Note that mortality due to subsistence harvest by people is additive, whereas pig predation is partly compensatory.

Scenario	Survival	Stage	Estimate	SE
Wet	Juvenile	$S_{1,5}$	0.930	0.0281
	Adult	$S_{2\text{-}4,6}$	0.930	0.0281
Dry	Juvenile	$S_{1,5}$	0.834	0.037
	Adult	$S_{2\text{-}4,6}$	0.834	0.037
Dry Harvested 20%	Juvenile	$S_{1,5}$	0.834	0.037
	Adult	$S_{2\text{-}4,6}$	0.634	0.037
Dry harvested 30%	Juvenile	$S_{1,5}$	0.834	0.037
	Adult	$S_{2\text{-}4,6}$	0.534	0.037
Dry harvested 40%	Juvenile	$S_{1,5}$	0.834	0.037
	Adult	$S_{2\text{-}4,6}$	0.434	0.037
Dry Pig predation 48%	Juvenile	$S_{1,5}$	0.501	0.082
	Adult	$S_{2\text{-}4,6}$	0.501	0.082
Dry Pig Predation 58%	Juvenile	$S_{1,5}$	0.396	0.099
	Adult	$S_{2\text{-}4,6}$	0.396	0.099
Dry Pig Predation 73%	Juvenile	$S_{1,5}$	0.24	0.069
	Adult	$S_{2\text{-}4,6}$	0.24	0.069

earlier and at a smaller size than females (Kennett 1996). Estimates of male and female growth rates from the Giddadella site (Fordham *et al.* 2007a) were used in the model. Size of female maturity in *C. rugosa* is an evolved response that promotes demographic resilience under conditions of comparatively low survival (Fordham *et al.* 2007b). Small females (CL = 180-200 mm) were treated as mature in the model. Fecundity rate was derived as the product of mean clutch size (*m*), sex ratio (*sr*), proportion of reproductively active females (*r*) and hatchling survival (Φ_0). Clutch size is strongly correlated with body size (Fordham *et al.* 2007a). Mean clutch size for S_3 and S_4 was 10.18 and 14.01 respectively (number of clutches = 62 and 84). The proportion of reproductive females was set at 0.7 (range = 0.53 – 0.88; Fordham *et al.* 2007b) and we assumed a 50:50 sex ratio. Offspring sex of all chelid turtles so far examined is determined genetically (Georges 1988; Georges & McInnes 1998).

Φ_0 was derived as the number of hatchlings that hatch (*H*) divided by the number subsequently alive after one year (H_{t+1}). *C. rugosa* annually lay multiple clutches but, in almost all cases, only one clutch meets the narrow window of opportunity for hatching and emergence, defined by the onset of the monsoonal wet season, when rains soften the soil and fill the billabongs (Fordham *et al.* 2006a). As such, clutch frequency was set to one in the model. Hatching rates in *C. rugosa* are influenced by pre-incubation and incubation environment (Fordham *et al.* 2007d). We adopted a hatching rate (*hr*) expected under optimum incubation conditions. We did this to offset possible underestimation in hatchling production owing to our decision to set effective clutch frequency to one. *H* was calculated using the equation:

$$H = [(N_3 * m_3 * r)+(N_4 * m_4 * r)] * hr \qquad (3)$$

Density Dependence

Hatchling survival in *C. rugosa* is strongly density dependent, while adult survival and fecundity are density independent (Fordham *et al.* 2007b). Cormack-Jolly-Seber capture-mark-recapture analysis, prior to and after population manipulation at Imimbar and Ginmilly billabongs, and live-recapture and dead recovery (Burnham Models; Burnham

1993) analysis prior to and after a rare harvest event at Murrybulljuluk, allowed hatchling survival (Φ) to be estimated when population size (N) was at 32% ($\Phi = 0.30$), 43% ($\Phi = 0.10$), 78% ($\Phi = 0.14$) and 100% ($\Phi = 0.01$) of estimated carrying capacity (Fordham *et al.* 2007a,b). Hatchling survival at very low densities (1%) was assumed to be high ($\Phi = 0.93$; Table 7.1). The relationship between density and log survival was strongly linear ($r^2 = 0.936$) and thus a linear density dependent decay function was used to model the relationship between hatchling survival (HS) and N:

$$HS = a*Exp(b*N) \qquad (4)$$

where a is the intercept (a fixed at 1) and b is the slope ($b = -0.013$). As N increases, the rate of hatchling recruitment declines. This affects the realised population growth rate by negatively influencing F_3 and F_4.

Environmental Stochasticity

The wet-dry tropics of northern Australia experience extremes of high rainfall during the monsoonal wet seasons and the near absence of rainfall in the intervening dry seasons. The timing of the onset, duration and severity of the wet season dictates the presence or absence of water at wetlands at the end of the following dry season, in turn influencing *C. rugosa* survival (Fordham *et al.* 2006b). Local rainfall records for Maningrida (1980 – 2005; Australian Bureau of Meteorology unpublished data; see Figure 7.1b) were used to estimate drying frequency. If wet season rainfall exceeded 25% of the average (1290 mm), the year was classed as a ‘wet year’ and it was assumed that billabongs (waterholes) did not dry. This method resulted in 20 ‘dry years’ between 1980 – 2005, at a frequency of 0.77.

Pig Predation

In areas of high pig abundance, pig predation accounts for 96% of *C. rugosa* fatalities in dry years (CL > 100 mm; Fordham *et al.* 2006b). However, pig predation occurs at a time when this mortality is partially compensatory to other forms of predation and harvest (Fordham *et al.* 2006b, 2007a). Pig predation at Giddadella, in years of high pig abundance, occurred at an estimated rate of 48% of $S_{1\text{-}6}$ (CI = 23-72%; Fordham *et al.* 2007a) providing an additional 33% (CI = 7-58%) mortality above background rates. In some years pig predation maybe be as high as 73% (CI = 59-85%; Fordham *et al.* 2006b), causing an additional 56% (CI = 43-80%) mortality. At Damdam, pig predation was estimated to be 58% (CI = 36-78%; Fordham *et al.* 2007a) causing an additional 44% (CI = 21-63%) mortality.

Harvest

Drying, pig abundance and cultural activities regulate subsistence turtle harvesting. Harvesting only occurs in dry years, at sites where pig abundance is low (Fordham *et al.* 2006b). At Murrybulljuluk, a region of low pig abundance, people harvested some 20% of turtles with CL > 140 mm in annual harvest season (Fordham *et al.* 2007a). Aboriginal harvest rates are regulated by the frequency and timing of ceremonies and other cultural activities that interfere with harvests. We have observed that specific wetlands tend to be harvested in no more than 50% of dry years.

We modelled the commercial harvest of turtles (CL ≥ 140 mm), largely for the pet trade, as an annual post-breeding harvest, unrestricted by rainfall. We made the precautionary assumption that commercial harvest mortality was additive to other sources of mortality, though in reality predator interaction, owing to the timing of the harvest, would to an extent moderate the impact of additional harvest mortality (Kokko & Lindström 1998). It was further assumed that commercial harvesting could only occur at sites of low pig abundance, or in conjunction with effective localised pig eradication programs. As such, pig predation rate was set to zero. We did not simultaneously model commercial and subsistence harvesting because harvesting would have to be tightly regulated to guarantee sustainability – difficult if wetlands were harvested for subsistence as well as commercial purposes.

Model Scenarios

Separate matrices were constructed for (i) wet years; (ii) dry years; (iii) dry years with low pig abundance and no harvesting; (iv) dry years with high pig abundance; (v) dry years with subsistence harvesting; (vi) wet years with commercial harvesting; and (vii) dry years with commercial harvesting. The model was developed and simulated in Program *R* (*R* Development Core Team 2005). Stochastic simulations were projected over a period of 50 years, and the number of iterations was set at 1000. Initial population size was set at 99, and carrying capacity at 288 individuals, based on abundance estimates at Giddadella (Fordham *et al.* 2007b). Turtle density at Giddadella (3.1/ha; CI = 2.5-4.0) was low compared to populations such as Imimbar that are rarely harvested and rarely predated by pigs (10.4/ha; CI =8.6-13.2; Fordham *et al.* 2007b). The *R* model script is available from the authors on request.

We initially tested 4 scenarios to identify potential threats to population persistence:

(i) No pig predation or subsistence hunting.

(ii) Pig predation at a rate of 48%, 58%, and 73% of the total population size of turtles with CL > 100 mm.

(iii) Subsistence harvests at a rate of 20%, 30% and 40% of turtles (CL ≥ 140 mm) each dry year and in 50% of dry years.

(iv) Commercial harvests at a rate of 20%, 30% and 40% of turtles (CL ≥ 140 mm) each year and every second year.

The impact of subsistence turtle harvesting and pig predation on population persistence was also retrospectively simulated using the 26 year sequence of wet dry events in the Maningrida region, providing insight into the impact of extensive dry periods coupled with consecutive wet years (Figure 7.1b).

Flooding frequency in northern tropical Australia is predicted to increase in response to climate change (Nott & Price 1999), so we tested the frequency of wet years (refugial years) needed to support population persistence in regions of high pig abundance. Efficiency of ‘headstarting’ to offset harvest and pig predation was also tested. Headstarting describes the egg collection and captive hatching and rearing of turtles through a vulnerable period of their life cycle, whereupon they are released as supplemental individuals into their natural environment (Heppell *et al.* 1996a). *C. rugosa* is well suited to egg collection and incubation, and the captive growth of subsequent hatchlings (Fordham *et al.* 2007d). We estimated the number of additional yearlings needed to maintain population size at half of carrying capacity (approximately that achieved under a maximum sustainable yield model with logistic growth) in regions of high pig abundance and if populations were to be commercially harvested. Additional yearlings were calculated by averaging the sum of the maximum number of additional yearlings required per iteration.

Expected minimum size (EMS) was used as the main measure of risk to population decline for each scenario because it provides a better indicator of the threat of population decline than more commonly reported measures such as risk of extinction (McCarthy & Thompson 2001). We calculated EMS by taking the smallest population size observed for each iteration and averaging these minima; the output is equivalent to the area under the quasi extinction curve (McCarthy 2006). Population decline was measured as percentage decrease in EMS value from the initial population size (McCarthy & Thompson 2001). We also report the average median population size and the extirpation probability (EP) for each scenario.

Results

Pig Predation

Pig predation at all levels (48%, 58%, and 73%) is predicted to cause a marked decline in the population trajectories of *Chelodina rugosa* (Figure 7.2) and extirpation within 30 years (EP = 1; Table 7.2). The regularity of flooding would have to increase four fold to provide a sufficient number of refugial years to prevent population decline as a result of pig predation in dry years (Table 7.3).

Harvest

A 20% subsistence harvest of adult and sub-adult turtles (CL ≥ 140 mm), each dry year, represented no threat to population persistence (EMS = 76; 23% population decline). Harvesting at this rate in 50% of dry years had little impact on population size (EMS = 95; 4% decline). A harvest rate of 30% each dry year caused population size to decline substantially (EMS = 31.0; 69% decline), but harvesting in only half of all dry years at this

Table 7.2: Scenarios for future exploitation and predation of *Chelodina rugosa* based on population modelling. Expected minimum population size (EMS), population decline (percentage decrease in EMS value from the initial population size), projected median population size (1000 model simulations) and the extirpation probability (EP) are described for each scenario. Numbers in parentheses are 95% simulation quantiles. Note that populations can be subsistence harvested in dry years at a rate of 20%. If harvesting occurs in 50% of dry years, populations can be taken at a rate of 30% without threatening persistence. Pig predation will cause extirpation if management institutions are not implemented. It is sustainable to harvest turtle populations commercially at an annual rate of 20%, provided pig predation and subsistence harvest are absent.

Scenario		**EMS**	**Population Decrease (%)**	**Median Pop. Size**	**EP**
No harvest and no pig predation		**	**	203 (189-232)	0
Customary harvest every dry year	20%	76	23	94 (74-147)	0
	30%	31	69	46 (28-101)	0
	40%	0	100	0 (0-43)	1
Customary harvest in 50% of dry years	20%	95	4	142 (98-199)	0
	30%	76	24	120 (67-188)	0
	40%	44	55	88 (25-171)	0.045
Pig predation	48%	0	100	0 (0-10)	1
	58%	0	100	0 (0-0)	1
	73%	0	100	0 (0-0)	1
Annual commercial harvest	20%	72	27	77 (70-85)	0
	30%	0	100	12 (0-35)	1
	40%	0	100	0 (0-0)	1
Commercial harvest every second year	20%	97	2	150 (104-212)	0
	30%	73	26	118 (64-195)	0
	40%	22	77	59 (0-156)	0.356

** Population size increased

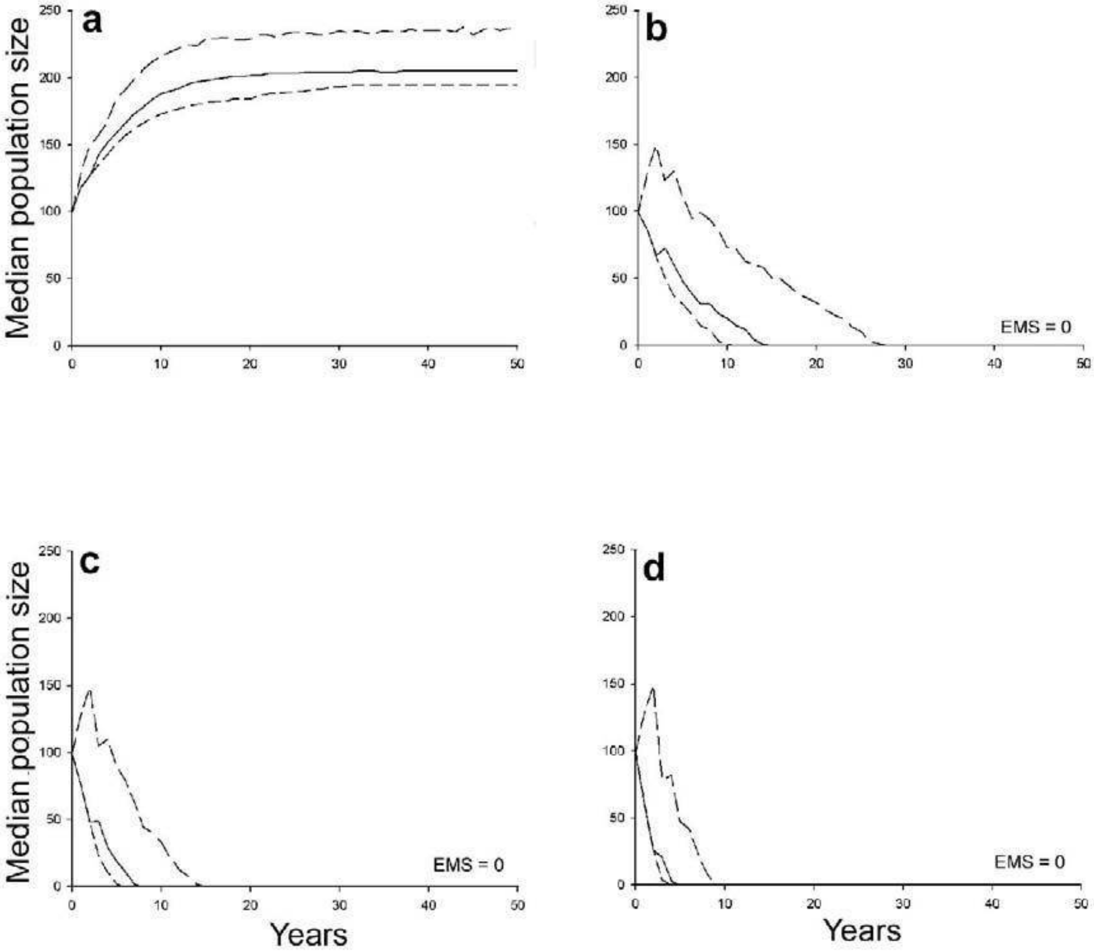


Figure 7.2: Projected median population size (1000 model simulations) and 95% quantiles in the absence of harvest and pigs (**a**) and when pigs prey on 48% (**b**), 58% (**c**) and 73% (**d**) of turtles (CL > 100 mm) immediately prior to each drying event.

Table 7.3: In regions of high pig abundance, the frequency of wet years (refugial years) would need to increase four fold to prevent population decline owing to pig predation. Expected minimum population size (EMS), population decline (percentage decrease in EMS value from the initial population size), projected median population size (1000 simulations) and the extirpation probability (EP) are described for each scenario (wet year frequency and pig predation rate). Numbers in parentheses are 95% simulation quantiles.

Wet Year Frequency	**Pig Predation Rate**	**EMS**	**Population Decrease (%)**	**Median Pop. Size**	**EP**
Doubled	48%	7	93	24 (0-129)	0.776
	58%	0	100	0 (0-50)	0.995
	73%	0	100	0 (0-0)	1
Tripled	48%	58	41	129 (41-246)	0.016
	58%	20	80	73 (0-228)	0.453
	73%	1	99	0 (0-166)	0.962
Quadrupled	48%	96	3	255 (136-283)	0
	58%	89	10	244 (103-283)	0
	73%	61	38	220 (30-283)	0.042

caused extirpation (EMS = 0) and a severe population reduction (EMS = 44; 55% decline) when it occurred in only 50% of dry years. Therefore, subsistence harvesting at rates greater than 20% in all dry years threatens persistence (Figure 7.3). If harvesting is conducted in 50% of dry years, populations can be harvested at a rate of 30% without threat of extirpation (Figure 7.3). The retrospective projection based on the sequence of flooding events observed in the Maningrida region over the past 26 years confirmed that subsistence harvesting at a rate of 20% is sustainable, even when nine consecutive dry (harvested) years occurred (Figure 7.4).

If pig predation and subsistence harvests are nonexistent, the model predicts that *C. rugosa* (CL ≥ 140 mm) can be harvested commercially at an annual rate of 20% without any threat of extirpation (EMS = 72; 27% decline: Table 7.2; Figure 7.5), or at 30% if harvesting occurs every second year (EMS = 73; 26% decline). Commercially harvesting at a rate of 40%, even if conducted only every second dry year, resulted in severe population decline (EMS = 22; 77% decline: Table 7.2).

Headstarting Hatchlings

The annual release of 59 yearlings would be enough to prevent extirpation in turtle populations that incur a pig predation rate of 48% (EMS = 97; 2% decline: Table 7.4). Annually releasing 70 yearlings would offset a pig predation rate of 58% (EMS = 96; 3% decline), while 87 yearlings would be need to offset a 73% predation rate (EMS = 92; 7% decline). Turtle populations could be harvested commercially at annual rates of 30% and 40% if 38 and 55 yearlings, respectively, were released into the population each year (Table 7.4). Therefore headstarting programs provide an effective conservation strategy for *C. rugosa* populations in regions of high pig abundance (Figure 7.6) and could be used to increase commercial or traditional harvest yields of adults.

Discussion

Freshwater turtle harvesting has been widely criticised because of unfavourable life history traits (Cunnington & Brooks 1996; Heppell 1998) and a presumed negligible compensatory response to harvest (Congdon *et al.* 1993, 1994). We clearly demonstrate

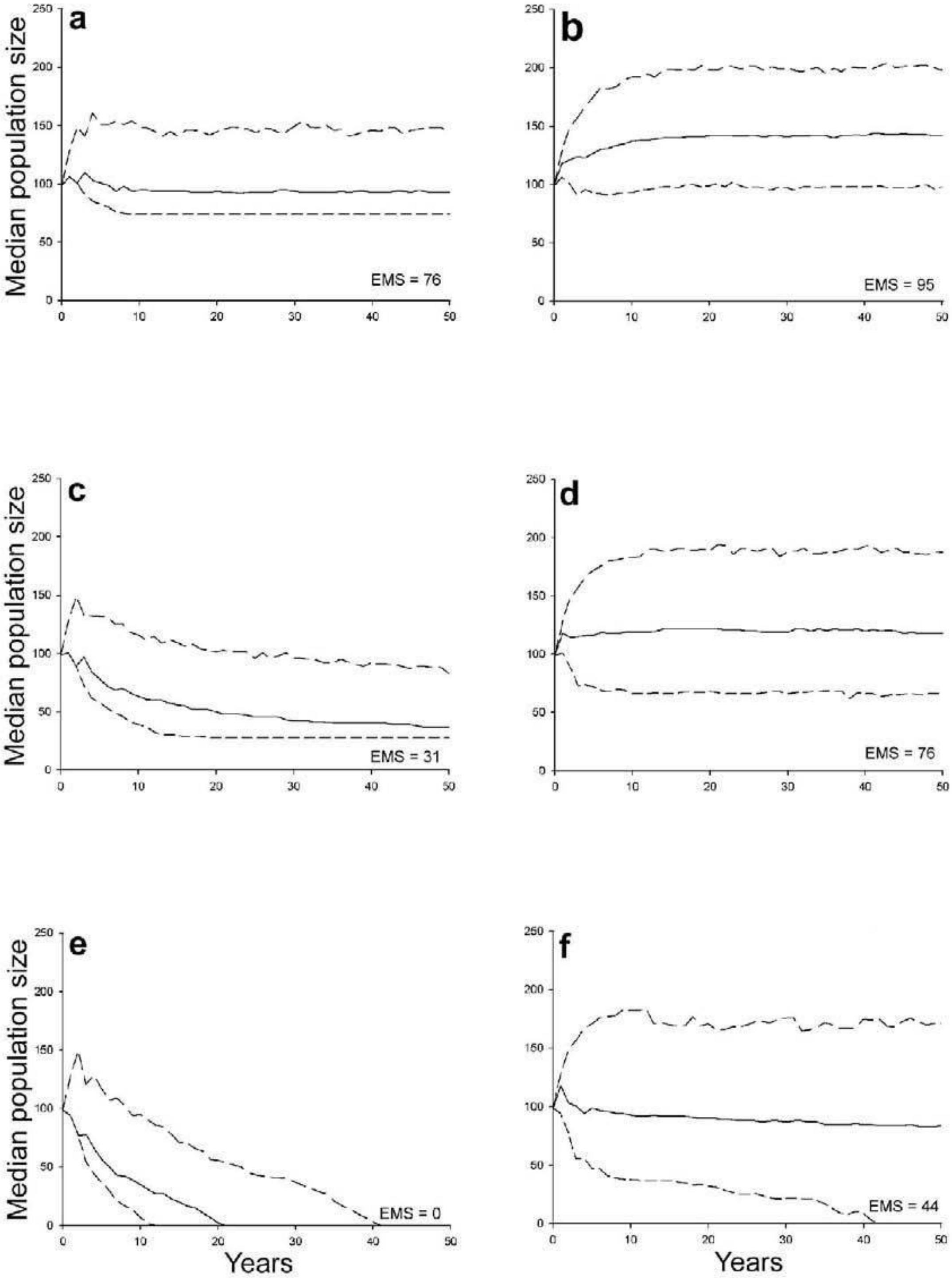


Figure 7.3: Projected median population size (1000 simulations) and 95% quantiles under different rates and frequencies of subsistence harvesting. Harvest rates were simulated as a proportion of the turtle population (CL ≥ 140mm) at rates of 20% (**a**, **b**), 30% (**c**, **d**) and 40% (**e**, **f**) every drying event (**a**, **c**, **e**) and in 50% of drying events (**b**, **d**, **f**).

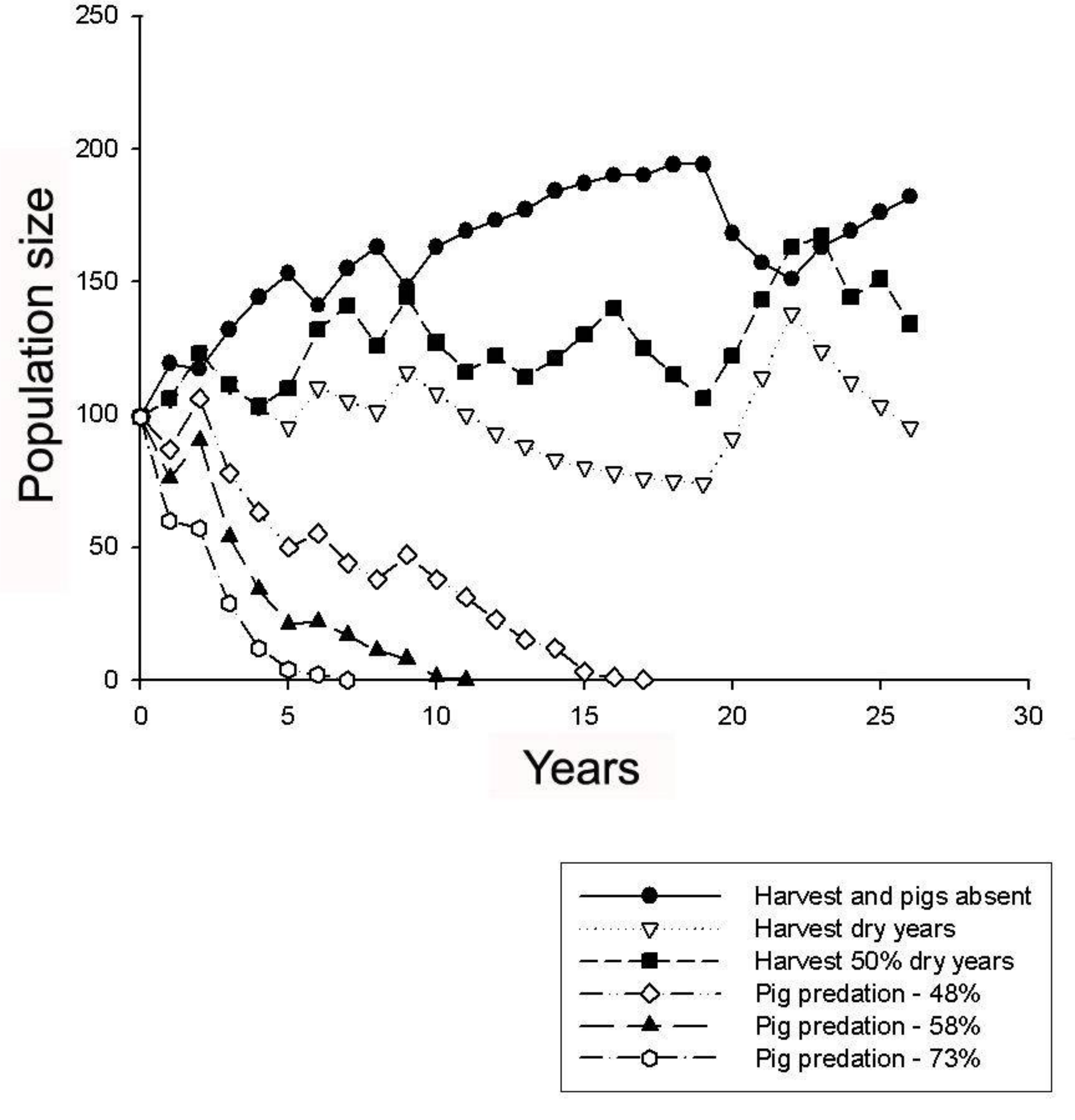


Figure 7.4: Population size estimated retrospectively from a starting size of 99, based on a 26 year sequence of wet and dry years in Maningrida, northern Australia. Harvest rate was set to 20% (CL ≥ 140 mm) in dry years. Note that harvesting in dry years was sustainable even when nine consecutive dry years occurred (years 11 – 19).

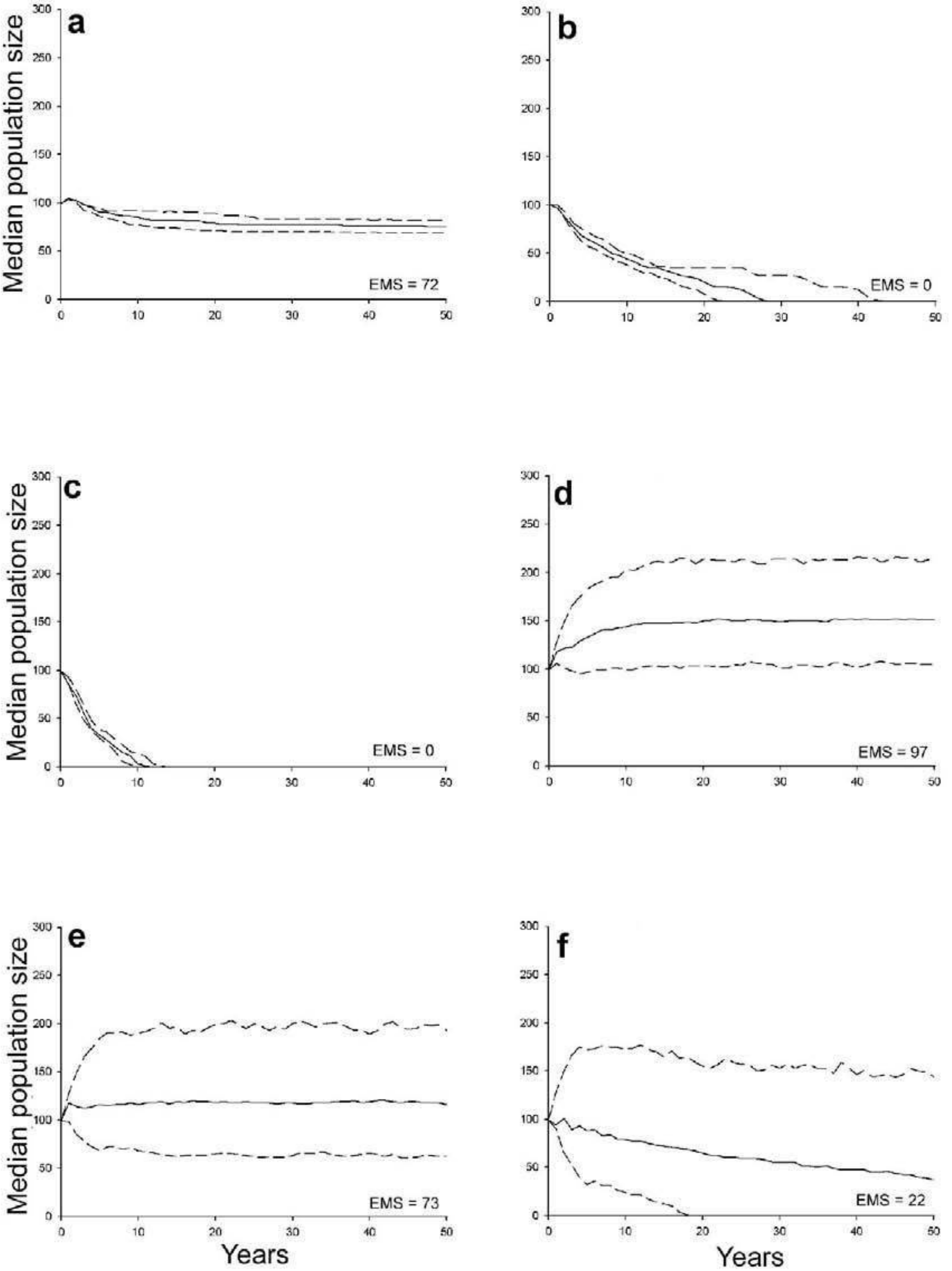


Figure 7.5: Median population size (1000 simulations) and 95% quantiles with sub-adult and adult turtles (CL ≥ 140 mm) commercially harvested at rates of 20% (**a**, **b**), 30% (**c**, **d**) and 40% (**e**, **f**) annually (**a**, **c**, **e**) and every second year (**b**, **d**, **f**).

Table 7.4: Number of additional yearlings needed to offset pig predation and annual commercial harvesting when population size is set at half carrying capacity (MSY). Expected minimum population size (EMS), population decline (percentage decrease in EMS value from the initial population size), projected median population size (1000 simulations) and the extirpation probability (EP) are described for each scenario. Numbers in parentheses are 95% simulation quantiles.

Scenario		**Additional Yearlings**	**EMS**	**Population Decrease (%)**	**Median Pop. Size**
Pig predation	48%	59	97	2	116 (97-143)
	58%	70	96	3	107 (90-139)
	73%	87	92	7	97 (66-134)
Annual commercial harvest	20%	23	**	**	138 (123-170)
	30%	38	98	1	131 (108-170)
	40%	55	97	2	120 (97-143)

** Population size increased

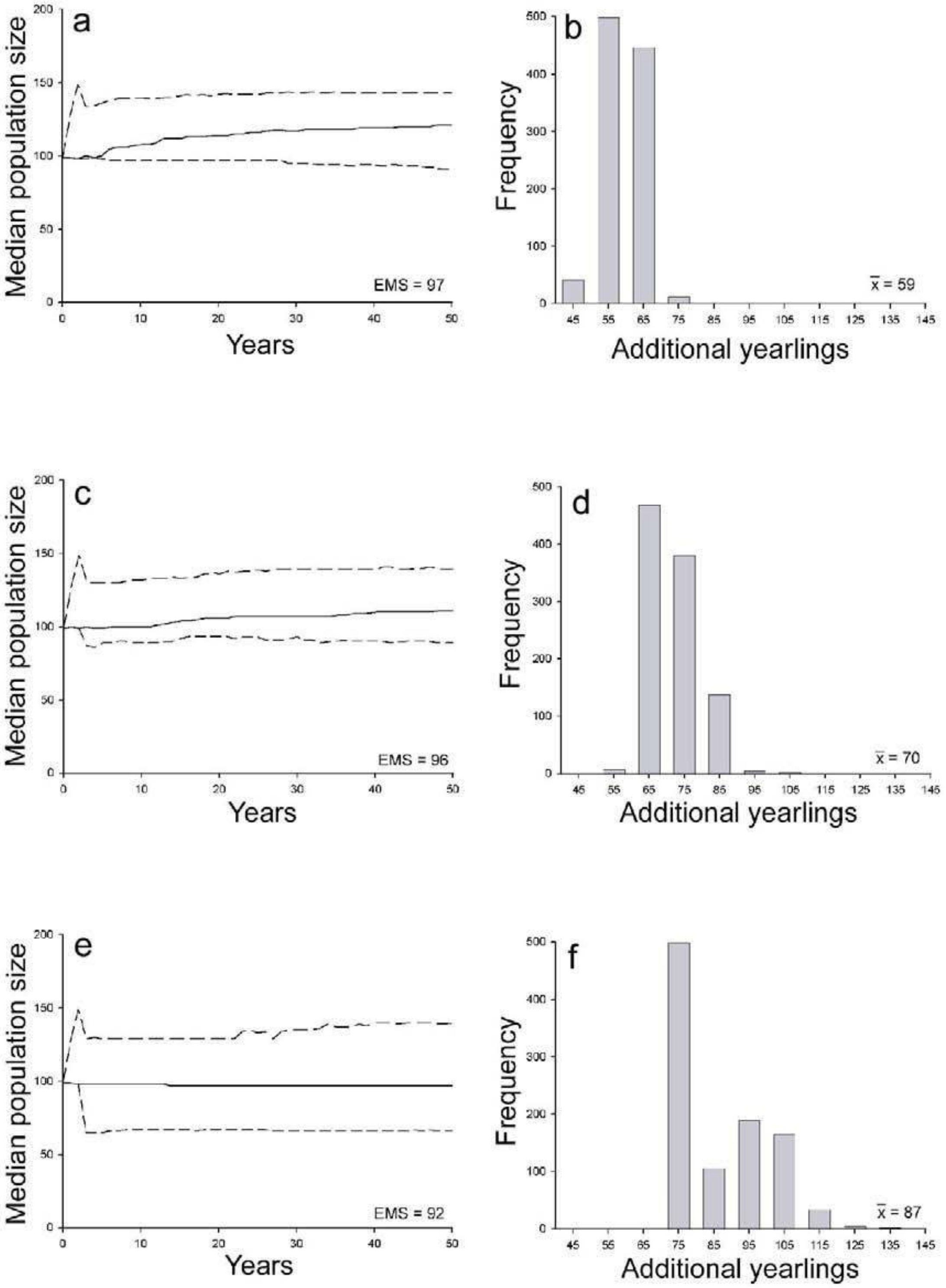


Figure 7.6: Yearling supplementation provides an efficient management strategy to offset turtle predation by pigs. Adding 59 yearlings every dry year would guarantee persistence if pigs prey on 48% of turtles (**a**, **b**); adding 70 yearlings would offset a predation rate of 58% (**c**, **d**); adding 87 yearlings would offset a predation rate of 73% (**d**, **e**). Median population size and 95% quantiles are plotted for each scenario. Histograms show the maximum number of yearlings needed to maintain the population at half carrying capacity in each simulation iteration (see Methods).

that *Chelodina rugosa* populations have the capacity to compensate for a reasonably high level of sub-adult and adult harvesting (subsistence and commercial), owing to traits that support rapid recovery, particularly the strong feedback between hatchling survival and density. Density dependent mechanisms, such as increased growth, fecundity and survival when intra-specific competition is low, do not necessarily need to operate amongst adult turtles to prevent population decline, as has been alleged (Converse, Iverson & Savidge 2005). However, we do show that turtle predation by pigs, if left unmanaged, is so high that the extirpation of many *C. rugosa* populations in the near future is all but assured. Management strategies to reduce or offset turtle predation by pigs are therefore an urgent conservation priority.

Aboriginal harvest rates are regulated by stochastic rainfall, the frequency and timing of ceremonies, and other cultural activities that interfere with harvests (Fordham *et al.* 2006b). Recently, we suggested that these refugial years might be important for maintaining harvested *C. rugosa* populations over the long period of interaction with people in tropical northern Australia (Fordham *et al.* 2006b, 2007a). The model projections presented here, demonstrate that a 20% harvest of sub-adult and adult *C. rugosa* (CL ≥ 140 mm) is sustainable (Figure 7.3), even when extended, or even continuous, periods of consecutive dry years occur (Figure 7.4; Table 7.2). Subsistence harvest rates as high as 30% are sustainable if harvest, owing to cultural responsibilities, occurs in only half of all possible dry years (Figure 7.3). Therefore, density dependent hatchling survival, vital life history traits (fast somatic growth and a small size of female maturity; Fordham *et al.* 2007a), and refugial years, all play an important role in compensating subsistence harvests.

Our model projections indicate that the local persistence of many *C. rugosa* populations in northern tropical Australia are under severe threat owing to heavy predation by pigs. A potentially conservative estimate of future pig predation (48% of turtles with CL > 100 mm predated each dry year) resulted in turtle extirpation in less than 30 years (Figure 7.2). The interaction between pig abundance and *C. rugosa* survival is related to vegetation structure and timing of drying (Fordham *et al.* 2007a). Although dispersal rates of *C. rugosa* between woodland savannah billabongs are low (Fordham *et al.* 2006a, 2007a), local cyclonic activity and consecutive years of high rainfall induce rare episodes of inter-population movement (Fordham unpublished data). Theoretically, spatial structure and population refugia could potentially play a role in regulating pig-predated populations (McCullough 1996; Brook & Whitehead 2005b), However, dispersal-based compensation from refugial sites would need to be extremely frequent to counter rapid population decline at sites where predation by pigs is common. Given that the magnitude and frequency of extreme flooding events is expected to rise in northern tropical Australia (Nott & Price 1999; Hughes 2003), *C. rugosa* may benefit from climate change via an increased frequency of inundation years, and increased episodes of between-population movement. In the absence of any possible increase in recruitment through immigration, the frequency of refugial years would need to experience a four-fold increase to compensate pig predation in dry years (Table 7.3).

Just 35 years ago, *C. rugosa* yields were relatively high in Arnhem Land (Russell-Smith *et al.* 1997) and pigs, based on Aboriginal harvest rates, were in all probability, locally rare or non-existent (Altman 1984). It is likely that pig populations, owing to a short history of colonisation in Arnhem Land, are yet to reach carrying capacity. Thus, without appropriate management, turtle predation rates by pigs are expected to rise (Fordham *et al.* 2006b). A multi-facet management program, combining pig predation minimisation strategies (culling and fencing) and strategies that offset pig predation (headstarting), will be critical if we are to prevent the extirpation of most *C. rugosa* populations found in regularly drying savannah billabongs. Turtle predation by pigs is periodic, occurring during the weeks immediately prior to drying (Fordham *et al.* 2006b). Localised culling of pigs during this period enhances turtle survival (Fordham unpublished data), promoting population persistence. Spatial and temporal heterogeneity influences when wetlands dry (Fordham *et al.* 2007a), and thus, a versatile, highly co-ordinated culling approach will be needed to ensure the persistence of *C. rugosa* populations at the landscape scale. At a local level, pigs could be fenced out of billabongs of customary importance, eliminating pig predation, allowing subsistence harvesting to occur without threat of extirpation. Facilitating land occupation by outstation residents (people heavily involved in subsistence activities) would also benefit *C. rugosa* conservation, because it would augment feral animal control (Altman & Cochrane 2005).

The efficiency of headstarting turtles to mitigate the effects of adult mortality has been criticised (Frazer 1992), because management effort focused on increasing first year turtle survival is perceived to be unlikely to promote population growth if sub-adult and adult survival remains low (Heppell *et al.* 1996a). Yet more recent evidence suggests that there is merit in efforts focused on increasing egg and hatchling survival (Dutton *et al.* 2005). We show that supplementing populations of freshwater turtles with additional yearlings provides a viable method to offset pig predation (Figure 7.6). Long-lived species with 'fast' recruitment that occupy relatively small discrete isolated populations, such as *C. rugosa*, are well suited to prosper from headstarting. Thus, generating the number of additional yearlings needed to have a positive impact on first year survival in these *C. rugosa* populations ($N < 300$; Fordham *et al.* 2007b) is reasonably feasible (Table 7.4).

Unsustainably high levels of harvesting for human consumption are directly responsible for the precarious conservation status of many species of turtle (Klemens & Thorbjarnarson 1995; Gibbons *et al.* 2000). Nevertheless, if appropriate management institutions are implemented, harvesting of long-lived reptiles can be sustainable (Bradshaw *et al.* 2006). For example, if turtle predation by pigs is minimised and subsistence harvesting is forfeited, commercial harvesting of adult and sub-adult *C. rugosa* (CL ≥ 140 mm) at an annual rate of 20% is sustainable, and a rate of 30% would not threaten persistence if harvesting occurred every second year (Figure 7.5). Moreover, headstarting hatchlings could be used to increase harvest yields (Table 7.3). If managed correctly, the commercial harvest of sub-adult and adult *C. rugosa* could provide a rare example of a biologically sustainable turtle industry.

The significance of our findings are broad because they challenge the prevailing view that sustained sub-adult and adult survival is crucial for achieving long-term population stability in freshwater turtles (Brooks, Brown & Galbraith 1991b; Congdon *et al.* 1993, 1994; Cunnington & Brooks 1996; Heppell 1998; Converse *et al.* 2005; Spencer & Thompson 2005). Furthermore, our research provides both empirical and predictive evidence to show the conservation threat that pigs pose to *C. rugosa*. Even conservative estimates of pig-related turtle mortality exceed what can be compensated by increased hatchling survival, and will assuredly lead to severe population declines.

Feral animals often constitute a culturally and economically important resource for indigenous people (Altman 1982; Bowman & Robinson 2002), creating a management paradox (Brook *et al.* 2006; Fordham *et al.* 2006b). Our research on feral pig impacts on freshwater turtles is currently being used to inform indigenous communities of the threat pigs pose to the persistence of *C. rugosa*. Moreover, our modelling provides a way to estimate the likelihood of success of a range of available management solutions, enabling collective informed conservation decisions to be made at a local level. A multi-pronged management approach of periodic local culling of pigs, fencing of wetlands and headstarting hatchlings will ameliorate the threat faced by many *C. rugosa* populations of importance to indigenous people of tropical northern Australia. If successfully implemented, such interventions should allow *C. rugosa* harvests to continue into the future, as they have for countless generations.

Chapter 8

Synopsis

Pictures: Conserving *Chelodina rugosa* harvests into the future [A.Georges, D.Fordham]

Synopsis

Research findings described in previous chapters are inter-related and, when taken together, they fulfil the primary aims of my doctoral thesis. These findings provide the fundamental science necessary to underpin an indigenous enterprise focused on the harvest of *Chelodina rugosa* and give fresh scientific insights relevant to ecology, conservation and environmental management. Industry outputs include providing optimal conditions for the storage and incubation of *C. rugosa* eggs and husbandry of hatchlings, and valuable information on the population dynamics of *C. rugosa*, allowing informed decisions on levels of harvests that are biologically sustainable and the offsets that can be put in place to increase harvests. Furthermore, my research will contribute considerably to advances in science, demonstrating a diversity of developmental responses to environmental variability in *C. rugosa*, possibly providing a unique amniote model for the study of evolutionary responses to stochasticity in variables that govern timing of reproduction, duration of development and timing of hatching and emergence. I have demonstrated a strong compensatory interaction between hatchling survival and population density in *C. rugosa* which, coupled with evidence of life history attributes somewhat unusual for turtles (rapid growth, early maturity), promote demographic resilience under conditions of comparatively low survival. My research thus throws into question previous conclusions from modelling of chelonians where compensatory responses were assumed not to occur (Congdon, Dunham, van Loben Sels 1993, 1994; Doak Kareiva & Klepetka 1994; Cunnington & Brooks 1996; Heppell, Crowder & Crouse 1996a; Heppell *et al.* 1996b; Chaloupka 2002; Heppell 1998; Converse, Iverson & Savidge 2005). These I believe are the substantial and original contributions made in my thesis. I elaborate on these contributions below, and draw together linkages between them.

Egg Inundation, Incubation and Hatchling Husbandry.

C. rugosa can nest underwater (Kennett, Christian & Pritchard 1993a; Kenett, Georges & Palmer-Allen 1993b; Kennett, Christian & Bedford 1998). The results presented in Chapter 2 carry the findings further, by demonstrating that eggs of *C. rugosa* can survive at least 25 weeks inundation, almost six months, with an optimal inundation duration of 6 weeks.

Eggs not held under water suffer the same mortality as eggs inundated for 25 weeks, suggesting that underwater nesting is not a facultative capacity but rather, inundation is essential for optimal survival of embryos. There is likely to be strong selection for hatchling survival (Seymour & Ackerman 1980), so these findings indicate that *C. rugosa* routinely nest under water in the shallows, and thus, exhibit a unique breeding strategy. Nesting in a water depth of 14 cm, utilising a shallow nest chamber depth of 10 cm (Kennett *et al.* 1993a) maximises embryo survival in the absence of rainfall after nesting. Another remarkable finding was that inundation duration has a profound effect on incubation period, reducing it by up to 9 weeks over what would be expected at a given temperature. Eggs inundated for up to 7 weeks complete incubation faster than had they been laid at the same time in dry ground. The complexity of incubation in this species is usually the domain of lower vertebrates facing similar environmental challenges in the variables that govern timing of reproduction, duration of development and timing of hatching and emergence (Wourms 1972a,b,c). A more extensive exploration of embryonic arrest in *C. rugosa*, and the expression of these traits under field conditions, offers an opportunity to advance our understanding of the co-evolution of nesting phenology, developmental duration and timing of hatching in vertebrates faced with great environmental stochasticity in the variables that influence reproductive success.

Developmental arrest in response to egg inundation in *C. rugosa* also benefits commercial egg harvesting because eggs can remain in diapause for up to 10 weeks without appreciable impact on egg or embryo survival, permitting eggs to accumulate until there are sufficient numbers to be incubated as batches. Embryonic diapause also allows eggs to be transported (under water) and sold into niche markets without incurring high levels of mortality. Such egg preconditioning can be combined with control over incubation and hatching environment to maximize the development and survival of embryos and subsequent hatchlings (see Chapter 3). The embryonic survival of *C. rugosa* is greatest at an incubation temperature of 26°C, steadily declining as temperature increases to 32°C. A similar increase in incubation temperature decreases incubation period by approximately 40 days; however almost half of this variation in incubation period is attributed to the increase in incubation temperature from 26 to 28°C. Integrating results of Chapters 2 and 3 suggests that inundation of eggs for 6 weeks (2-10 weeks is acceptable), incubation of embryos at 28°C and raising hatchlings in water at 28°C will yield the best overall outcomes for the turtle industry in Maningrida. These findings underpin a hatchling enterprise that not only contributes to economic self-sufficiency in a remote aboriginal community, but also employs young people in a way that is connected to traditional practices and indigenous knowledge, bringing them onto their traditional lands and providing tangible cultural benefits.

Subsistence Harvest and Pig Predation.

During turtle harvests in Arnhem Land today, harvesters constantly curse "too much pig" in exasperation over the futility of their harvest efforts. In Chapters 4 and 5, I quantitatively illustrate that contemporary harvest rates of *C. rugosa* in Arnhem Land are low, not because of over-harvesting or a cultural shift in the emphasis placed on turtle harvesting but, rather, because pigs deplete available stocks immediately before Aboriginal harvests. This substantiates the concerns of harvesters. Although predation by exotics on Australian native vertebrates has been argued as a source of population decline (Dickman 1996; Burbidge & Manly 2002), such inferences have lacked empirical evidence. This is particularly so for feral pigs in Australia. *C. rugosa* survival rates, quantified by radio telemetry (see Chapter 4) and capture-mark-recapture techniques (see Chapter 5) and modelled using projection matrix models (see Chapter 7) provide, to the best of my knowledge, the first empirically based predictive evidence in support of feral pigs directly threatening to extirpate a native vertebrate in Australia.

Cultural practices linked to the preparation of traditional foods provide important conduits for the generational transfer of traditional knowledge and cultural history (Freeman 1997). In Chapter 4, I predict that *C. rugosa* harvest efficiency in Arnhem Land, owing to predator competition with pigs, will continue to dwindle, suggesting that in the near future Aboriginal people may have no choice but to abandon the harvest of *C. rugosa*, an action that will have damaging cultural consequences. Adoption of contemporary harvest methods does not extinguish the cultural benefits of subsistence harvesting (Collins, Klomp & Birkhead 1996). In Chapter 5, I demonstrate that harvest yields would improve if contemporary harvest approaches were adopted, allowing harvesting to occur immediately before, and during, the early aestivation period, when pig predation takes place. However, model projections indicate that such harvest practices would be unsustainable, without a co-commitment to alleviating pig-related turtle mortality, because pigs are a highly successful predator of *C. rugosa*. Contemporary subsistence off-take only partially compensates turtle mortality caused by pig predation (see Chapter 7).

Population models illustrate that a broad management approach, encompassing periodic local culling of pigs, fencing wetlands (predation minimisation) and headstarting hatchlings (offsetting predation) will ameliorate the extirpation threat faced by many *C. rugosa* populations in low lying regions of savannah woodlands in Arnhem Land, allowing *C. rugosa* harvests to continue into the future as they have for countless generations. In unoccupied and thus unmanaged remote sections of Arnhem Land today, country viewed as ‘sick’ or ‘unhealthy’ (Otto Bulmaniya Campion, personal communications), many populations that were important harvest sites less than 30 years ago (Brian Njinawanga Campion, personal communications) are either no longer populated by *C. rugosa*, or numbers are so low that extirpation can be expected to occur in the near future (Fordham unpublished data). Based on the remoteness and vastness of Arnhem Land (97 000 km ^{2}), and the sheer number of *C. rugosa* populations threatened with extirpation, I suggest that management actions should be concentrated, targeting sites of cultural importance. This approach will inevitably result in the extirpation of some *C. rugosa* populations. In defence of a focused conservation effort, I highlight that extirpation is already happening.

Feral animals often constitute a culturally and economically important resource for indigenous people (Altman 1982; Bowman and Robinson 2002), and thus, constitute a management paradox (see Chapter 4). This thesis will alert Aboriginal communities and scientists to the threat pigs pose to the persistence of *C. rugosa* in low lying savannah regions of Arnhem Land, enabling informed collective conservation decisions to be made at the community level.

Compensatory Density Dependent Processes in Freshwater Turtles

A perception prevails that the harvest of sub-adult and adult chelonians is inherently unsustainable, and therefore unacceptable (Doak *et al.* 1994; Cunnington & Brooks 1996; Heppell *et al.* 1996a,b). Turtle life history traits such as low egg and hatchling survival, slow growth, late maturity, high juvenile and adult survival and a potential for long lifespans, limit the ability of freshwater turtle populations to spring back after population depression and constrain their ability to resist chronic increase in adult mortality (Brooks *et al.* 1991; Congdon *et al.* 1993, 1994; Heppell 1998; Converse *et al.* 2005). In Chapters 5 and 6, I demonstrate that while it may be that high rates of survival are crucial for some freshwater turtle species, the life history traits and population dynamics of other species, such as *C. rugosa*, better equip them to compensate some level of increased mortality through predation or harvest.

Chapter 5 establishes a correlation between the intensity of sub-adult and adult turtle mortality (caused by pig predation and indigenous harvesting) across waterholes and key life history parameters, which indicates that *C. rugosa* may compensate for low rates of survival via increases in hatchling recruitment, decreases in female size of maturity and increases in postmaturity growth. Correlative analyses allow causality to be inferred (cautiously), but manipulative studies are needed to demonstrate causation (Cappuccino & Harrison 1996). In Chapter 6, I experimentally illustrate the demographic processes that underlie population regulation in *C. rugosa* by manipulating sub-adult and adult densities (reduction and supplementation), concluding that hatchling recruitment responds positively to a downward displacement in population density. Model projections in Chapter 7 confirm that sub-adult and adult *C. rugosa* can incur annual harvests of up to 20 % without threat of extirpation, owing to ‘fast’ life history traits (fast growth and a reduced size of maturity) and a strong interaction between hatchling survival and density. Viewed together, these chapters negate the universal generality of turtle vulnerability to sub-adult and adult harvesting, presenting an open challenge to the wide-ranging perception that freshwater turtles do not display density dependent responses (Brooks *et al.* 1991b; Congdon *et al.* 1993, 1994) and that high sub- adult and adult survival is crucial for achieving long-term population stability (Cunnington & Brooks 1996; Heppell 1998).

Commercial Harvests of Freshwater Turtles

Demonstrating a level of resistance to sustained harvest and resilience to negative perturbations in abundance in *C. rugosa* is a discovery that will potentially transform present approaches to turtle conservation and management. This finding, although supportive of turtle harvests, does not advocate a broad pro-harvest mandate for all freshwater turtles. In Chapter 3, and subsequent chapters, I acknowledge the threat human exploitation and development-related pressures pose to many freshwater turtles (Klemens & Thorbjarnarson 1995; Gibbons *et al.* 2000). The situation is particularly acute for Asian freshwater turtles, where many species are endangered or critically endangered, largely because of over exploitation for the food and medicine market (van Dijk *et al.* 2000). Nevertheless, I argue that the high attention turtles are receiving in the conservation arena because of the Asian turtle trade has led to a level of opposition to the view that turtles, similar to other long-lived organisms such as condricthyans (Walker 1998; Stevens *et al.* 2000), display a differential vulnerability to exploitation. Seminal papers that employ deterministic life history analysis to evaluate harvest suitability (Congdon *et al.* 1993, 1994; Heppell 1998) continue to be used to caution the removal of even a small fraction of adults because of the threat of unacceptable population decline (e.g., Galbraith, Brooks & Brown 1997; Reed & Gibbons 2003; Schlaepfer, Hoover & Dodd 2005). Recommendations such as these will in many cases provide a sound conservation policy but, as shown in Chapters 5-7, species with 'fast' life histories afford a level of sub-adult and adult harvest, owing to a compensatory increase in hatchling recruitment. Failure to recognise a differential vulnerability to turtle exploitation runs a risk of providing misleading prescriptions to conservation management. For example, harvests of *C. rugosa* would be deemed unsustainable, forfeiting a rare economic opportunity for the Maningrida community; in reality *C. rugosa* are resistant to a level of sub-adult and adult harvest, commercial or otherwise.

The scattergun strategy used by *C. rugosa* to cope with unpredictability in the onset of the period suitable for hatchling emergence and survival (see Chapter 2), favours sustainable egg harvests of *C. rugosa* at levels that are commercially viable. Mature female *C. rugosa* annually lay up to 5 clutches of eggs (see Chapter 5), exceeding previous estimates (up to 3 clutches; Kennett 1999). Many of these clutches do not meet the narrow hatching target (see Chapter 2) and thus the hatching success of *C. rugosa* eggs in the wild is extremely low. High levels of nest predation by *Varanus mertensi* (Mertens Water Monitor; Glauert 1951) further compounds hatching success (Fordham unpublished data). Therefore, industry egg harvests, intermittently spaced across the breeding season (up to 6-7 months) and capped at one clutch per female, have a negligible impact on population growth because most clutches of eggs do not produce hatchling recruits in the wild. Moreover, expansion of the industry to commercial harvests of sub-adult and adult turtles would be sustainable if turtle predation by pigs is minimised and subsistence harvesting is forfeited in those sites selected for commercial harvest. If pigs are controlled, sub-adult and adult *C. rugosa* could be commercially harvested at a rate of 20% without threat of extirpation (see Chapter 7).

Achieving sustainability of human use of wildlife depends not only on biological traits, such as abundance and life history characteristics, but also on a host of social, cultural and economic factors (Kwan, Marsh & Delean 2006). As an ecologist, my primary aim was to provide original science to underpin a sustainable commercial harvest of *C. rugosa*. Models in chapter 7 provide the Maningrida community with the foundation to establish a management plan for *C. rugosa*, which focuses on averting the present extirpation threat by conserving the species for customary and commercial exploitation. The effective long-term execution of this management plan offers an interesting topic for further research.

Summary

Successful creation of an independent indigenous workforce, skilled with the expertise to expand the fledgling turtle industry in Maningrida is a major achievement of this research.

So too is the associated collaboration of the science community with BAC and the wider Maningrida community. Indirectly, this research has gone a long way to developing proficiencies needed to independently assess and monitor the sustainability of future contemporary land management decisions in the region, providing an important step towards resource ownership and, in turn, economic independence and self-determination for the Maningrida community. My research not only provides the foundations for the indigenous enterprise, but also highlights a need for a paradigm shift in turtle population management towards acknowledging that turtles, like many other long-lived organisms, display a differential vulnerability to exploitation. This revelation will have broad implications for turtle management and the sustainable use of long-lived organisms in general. In identifying the immediate extirpation threat pigs pose to many *C. rugosa* populations in Arnhem Land, I provide feasible management recommendations that advocate a dynamic approach to the conservation of *C. rugosa* in Arnhem Land, an approach that will conserve turtle harvests into the future.

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Errata

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Page 25; line 16: “±” not “+”

Page 27; line 1: ‘prior to” not “to prior”

Page 121; line 13: “Table 6.2” not “Table 6.1”

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