

Applying theories of life history and ageing to predict the adaptive response of Murray River turtles to climate change and habitat modification

Fiona K. Loudon* and Ricky-John Spencer

Water and Wildlife Ecology Group (WWE) and Native and Pest Animal Unit (NPAU), School of Natural Sciences, University of Western Sydney, Penrith South DC, Locked Bag 1797, NSW, 1797, Australia

*Contact- f.loudon@uws.edu.au

ABSTRACT

The Murray River has undergone considerable changes over the last 200 years and the floodplain and aquatic fauna have also changed dramatically. Introduced species, such as European carp (*Cyprinus carpio*), Red Foxes (*Vulpes vulpes*), and rabbits (*Oryctolagus cuniculus*) are the predominant species in most areas, however, freshwater turtles, despite extremely high nest predation from foxes, remain among the highest biomass of any vertebrate in the ecosystem. The secret is their resilience through adaptive changes of a life history pattern that is strongly density dependent, however, with ongoing habitat modification and human-induced climate change, they may be at the limit of this adaptive resilience which will potentially lead to significant declines in the coming years. This review assesses how climate change predictions will affect habitat in the Murray River over the next 100 years and identifies how turtles may respond to these changes. We also identify key areas where management can facilitate adaptive strategies of turtles to a rapidly changing environment.

Key words: Murray River; turtle, life history, evolution, climate, growth, telomere, senescence, ageing, aging, management.

Introduction

Appearing on the fossil record more than 200 million years ago (Near *et al.* 2005), turtles have persisted through widespread environmental change, such as the Cretaceous extinctions and subsequent ice ages. Their successful survival strategy is buoyed by their conservative body plan (Dodd 2002). Despite their success in enduring throughout major climatic changes, the impacts of humans, such as habitat destruction and the introduction of invasive predators, may now be threatening their survival globally (Bowkett 2009).

Turtles inhabit all continents except Antarctica and are facing significant conservation issues that are challenging their survival (Turtle Conservation Fund 2002). The major threats to turtles include habitat destruction, pollution, disease, and over-exploitation for meat consumption or various body parts (Wilson and Tisdell 2001). In addition to this, most turtles will be exposed to a direct threat on their population demographics that will potentially cause their eventual extinction. With the majority of the world's turtles, as well as other reptilian species, experiencing Environmental Sex Determination (ESD), predicted warming events will not only affect their aquatic habitat, but also potentially eliminate males from populations if temperatures continually exceed pivotal temperatures during critical periods of incubation (Janzen 1994; Hulin *et al.* 2009).

With ESD, hatchling sex is determined by the environmental temperature encountered during the second trimester of development (Janzen 1994). Species differ in the

incubation ranges to produce a specific sex, with some producing females at both high and low temperatures and males at intermediate temperatures, while other species produce females at warmer temperatures and males at cooler temperatures or vice versa (Ferguson and Joanen 1983; Ewert and Nelson 1991). The pivotal or 'switch over' temperature range is less than 1°C for most species, meaning that small increases in incubation temperature can completely change the sex ratio of the clutch (Morjan 2003). With the threat of increased global temperatures, species with ESD may endure shifts in sex ratios that create an unsustainable population. An elevation of 4°C in central North America has the potential to alter sex ratio of painted turtles, *Chrysemys picta*, to the extent of all males being eradicated, effectively making the species reproductively redundant, or a 2°C rise in temperature severely skewing sex bias (Janzen 1994). ESD has been linked to the extinction of dinosaurs (Miller *et al.* 2004) and although turtles endured through the Cretaceous extinctions (Near *et al.* 2005), it remains unclear whether they may persist through future climate change events. Climate change modelling on turtle species has largely focused on its potential effects on sex ratios at the incubation stage; however the effects of rapid changes in climate, combined with increased human activity in freshwater environments, will have far more immediate and significant impacts than skewed sex ratios in a life history stage that already suffers extremely high rates of mortality. Turtle populations with ESD have undergone sex biases over several successive seasons (Janzen 1994), but the life history strategy of slow growth and late on-set

of maturity, incorporated with the longevity of the species, minimises the long term, threat of skewed sex ratios that would otherwise affect earlier maturing and short-lived species. Besides, in a heterogeneous nesting environment, small changes in nesting behaviour (eg. nesting earlier or in different locations) can dramatically affect incubation temperatures.

All but one Australian freshwater turtle, the pig-nosed turtle, *Caretchelys insculpta*, has genetically dependent sex determination and much of the current body of scientific literature on the potential impact of climate change on freshwater turtles is largely irrelevant to Australian populations. Regardless, if turtles with ESD persist, there will be other environment challenges that they will still have to overcome as global changes in climate occur. As ectothermic animals, growth, digestion, metabolism, reproduction and activity are all closely related to temperature in turtles. In addition, changes to water levels in lakes, rivers and wetlands may severely impact access to suitable habitat and nest sites, as well as increasing their exposure to predators and human interactions. The conservative life history evolution that enabled them to persist through environmental changes in the past may render them unable to adapt rapidly to the multitude of environmental changes that have occurred over the last 200 years and are predicted to occur into the future. Critically, increases in mortality to each life history stage of turtles (eg. nest predation from foxes on eggs; reduction of permanent water and habitat from drought, climate change or water diversions; increased disease and parasitic loads from increased salinity) may lead to population declines (Spencer and Thompson 2005), but changes in mortality can also be sources of selection and/or adaptation to increase population resilience (Spencer *et al.* 2006).

In this review, we predict the impact that both climate change and human activity may have on Murray River turtles. We limit our review primarily to the effects of changes to water regime and temperature. The focus of the study will take an adaptive point of view by assessing how individual life history traits, from molecular to population levels, might respond to changes of habitat and temperature based on basic demographic and thermal principles. While the focus of the study is on freshwater turtles of the Murray River, many of the principles and management recommendations should also apply to other major predators in the system, such as Murray Cod (*Maccullochella p̄eehi p̄eehi*) and Golden Perch (*Macquaria ambigua ambigua*).

Turtles in the Murray River

Three species of turtles live in the Murray Catchment: the broad-shelled turtle, *Chelodina expansa*, the eastern long-necked or snake-necked turtle, *Chelodina longicollis*, and the Macquarie or Murray River turtle, *Emydura macquarii* (Michael and Lindenmayer 2010). Although all three species spend the majority of time in water, they will travel over land to other water bodies or to lay eggs, making themselves as well as their eggs, vulnerable to predation by the European Red fox, *Vulpes vulpes* (Spencer *et al.* 2006; Michael and Lindenmayer 2010). All three are amongst the oldest maturing and longest living freshwater species in the world (Shine and Iverson 1995). The two

long necked species are obligate carnivores, whereas *E. macquarii* is omnivorous, consuming large volumes of filamentous algae or aquatic macrophytes (Spencer *et al.* 1998). All three species are found in permanent lakes, lagoons or oxbows of the River itself (Chessman 1988), but *C. longicollis* will also exploit temporary water bodies in large densities (Iverson 1982; Chessman 1988). When water levels are low, turtles will traverse over land in search of other water bodies or they can bury into the mud and enter long periods of aestivation until water levels increase after rain (Michael and Lindenmayer 2010).

Climate change and the Murray River

The Murray River forms part of the Murray-Darling basin, a highly important agricultural resource which covers 14% of Australia (Wei *et al.* 2011). Over one third of Australia's food supply is generated from the Murray-Darling Basin area and an estimated \$5 billion gross agricultural output per year (Quiggin 2001). Large-scale irrigation settlements were introduced in the late 1800's to support the agriculture in the area, which is prone to highly sporadic, but low average rainfall (Quiggin 2001). Although supporting Australia's economy with the water diversions, the area has been negatively impacted by land degradation, river water and land salinity, decrease in water quality and loss of biodiversity (Quiggin 2001).

Since the introduction of large-scale irrigation to the system over a hundred years ago, local ecosystems were forced to adapt rapidly or change. Now, in addition to water diversions, the threat of increasingly warmer and dryer weather conditions that are predicted will mean that both the aquatic and floodplain environments will continue to change rapidly. CSIRO (2007) climate change predictions for the of the Murray-Darling basin will see increases in mean temperature and considerably less rainfall over the next hundred years. For the Murray River in particular, such predictions are that by 2030 the average annual temperature could increase by up to 1.6°C with rainfall dropping by up to 13% (CSIRO and Australian Bureau of Meteorology 2007). By 2070, the changes could be as much as +4.8°C and -40% rainfall annually. In addition to annual rainfall changes, an increase in evaporation levels, droughts, extreme winds and number of fire days is expected (CSIRO and Australian Bureau of Meteorology 2007). The general consensus is that the amount of free-standing water in the Murray River, ie. permanent water bodies, will continue to decline simply because of increased demand from agriculture and population growth (Khan 2008). Climate change will hasten these environmental changes.

Combined with a reduction in the number of permanent water bodies, shallower water levels will mimic potential effects of climate change, with increased water temperatures and densities of freshwater turtles and fish. Water quality in the Murray River may be reduced by lower flows and higher temperatures. Increased incidence of fire could impact on the surrounding vegetative ecosystem as well as contaminating catchment areas with sediment and debris. Inadequate rainfall and stream flows, may increase salinity levels (Beare and Heaney 2002) or increase water nutrient

levels coupled with increased temperatures may create optimal conditions for algal blooms or other harmful occurrences. Ultimately, decreases in important flooding events and runoff may impair the function of freshwater wetlands that provide habitat for many wildlife species (CSIRO and Australian Bureau of Meteorology 2007).

Adapting to Less Water

The consequences of reduced permanent water and longer intervals between flooding events should lead to an increase in turtle densities because lagoons and lakes will be shallower and rates of immigration from drying water bodies will increase. Combined with increased water temperatures, water quality is likely to reduce further and many lagoons and lakes may become more eutrophic. Productive environments are not necessarily negative for turtles, population and biomass density of snapping turtles, *Chelydra serpentina*, are significantly higher in habitats of relatively high primary productivity (Galbraith et al. 1988). Similarly, Murray River turtles, particularly *E. macquarii*, which consume large quantities of algae (Spencer et al. 1998), may also flourish if primary productivity increases, but the biomass of Murray River turtles are already amongst the highest in the world (Iverson 1982; Thompson 1983; Spencer and Thompson 2005). The question is will there be enough water/habitat to support the current populations that are already under severe predation pressure from introduced species? In answering this question, the effects of population density need to be considered to assess the true impact of climate change on Murray River turtle populations.

The current major threats to Murray River turtle populations are predation from introduced species (Thompson 1983) and rising salinity levels, which are directly impacting turtles through disease and parasites (Kingsford et al. 2011) and indirectly through loss of habitat. A large population decline was predicted to have already occurred because of long-term sustained nest predation since foxes were introduced around 200 years ago (Thompson 1993), however, densities are still extremely high and populations have adapted (or evolved) to extreme nest predation (Spencer et al. 2006). The key seems to relate to strong population density dependence that evokes strong competitive interactions because at high densities, survival of juveniles is highly dependent on body size (Spencer et al. 2006). The result is a significant physiological response that alters demographic parameters such as juvenile growth, which ultimately leads to life history adaptation or evolution.

Anthropogenic induced changes of demographic processes have the potential to induce adaptive changes to life-history strategies. So far, there are three examples of how density-dependence plays a major role in regulating Australian freshwater turtle populations. *Chelodina rugosa* in northern Australia rebounds rapidly after density reductions from harvesting and pig predation (Fordham et al. 2007). The population resilience occurs by an increase in hatchling recruitment and survival past juvenile stages (Fordham et al. 2007). Spencer and Janzen (2010) explored how an increase in juvenile density through the removal of

predators impacted population growth estimates and the strength of selection on stage-based life-history traits. Long-term impacts of a North American population of turtles, *C. picta*, in a major recreational site have increased adult mortality of turtles but decreased nest predation, resulting in higher juvenile recruitment which in turn has led to fast individual growth and early on-set of maturation (age at maturity has almost halved) ie. higher productivity (Spencer and Janzen 2010). Density-dependent selection for larger body size appears the mechanism behind this change in life history. The role of density-dependent selection as a possible adaptive strategy in turtles was first noted by Spencer et al. (2006), who experimentally induced counterintuitive growth patterns in *E. macquarii*. Juvenile growth rate is positively related to density because body size is the primary determinant of survival at high densities. In addition to this, growth rate is genetically determined, which also implies an adaptive and evolutionary based resilience.

With all life stages displaying some level of density dependence in several turtles, it is likely that changes of density because of reduced permanent water in the Murray River will induce similar adaptive responses to that in North America. Increased adult mortality and density dependent selection for rapid juvenile growth should lead to earlier maturation at a smaller size of Murray River turtles, which will increase the reproductive potential of the population. The caveat is that nest predation on the Murray River is likely to remain much higher than in the North American population, where human activity has not only impacted on adult survival, it has also reduced densities of nest predators (Spencer and Janzen 2010). Unless climate change negatively impacts foxes, the major nest predator of turtles in the Murray River, higher densities of turtles and a reduction in permanent wetlands may actually increase levels of predation because nests will be more concentrated, which in turn may stifle any adaptive mechanisms through increased juvenile growth rates as a response to increased densities.

Temperature is another factor that will obviously be affected with increasing drought and changes in the amount of permanent water. Impoundments in the Murray-Darling have changed the amount of and quality of naturally occurring floodplain wetlands (Kingsford 2000). Areas historically subjected to flooding events, are now unlikely to flood regularly, due to impoundments and from the wetland (Kingsford 2000). Even with artificially maintained water bodies, higher evaporative rates and drier conditions predicted by climate change models will decrease the volume of permanent lagoons, and increase productivity to levels that will make many uninhabitable because water temperatures will promote blue-green algal blooms that may persist throughout the year. Being ectothermic, physiological processes such as growth and metabolism in turtles will also increase with increasing water temperatures, further enhancing the rate of adaptation. However, as water holes dry, turtles will starve and their exodus to search for new habitat will increase mortality rates. Adult survival is important for long-term sustainability of turtle populations (Spencer 2002b) and if populations that are already stressed, a loss of a small proportion of adult females could result in the population decline predicted by Thompson (1993).

Physiological Adaptations

Coltman (2008) argued that adaptation and rapid contemporary evolution occurs in response to invasive species, habitat degradation, climate change, and exploitation, but if adaptation or evolution is to occur amongst Murray River turtles, some major physiological changes will be associated with increased growth rates and earlier maturation. Much of the research on anthropogenically induced adaptation or evolution of organisms lies in theoretical and experimental considerations of ageing and fisheries research, such as commercial fishing practices inducing a reduction in the age and size at which fish mature (Swain *et al.* 2007). The theory of ageing is based on a life history trade-off between an investment in maintenance or investment in growth and reproduction (Monaghan and Haussmann 2006; Robert and Bronikowski 2010). Ageing occurs on both a cellular and organismal level whereby the physiological capabilities of an organism diminishes over time, culminating in senescence and eventually death (Robert and Bronikowski 2010). In unstable environments, an organism may divert resources towards rapid growth and early reproduction at the expense of maintenance because mortality rates are high (Robert and Bronikowski 2010). In contrast, in stable environments, where survival rates are high, organisms may favour delayed maturity (at a larger body size) to increase lifetime fecundity (Robert and Bronikowski 2010).

The ecological advantages to rapid growth increasing body size as fast as possible include the reduction of risk of predation and increased reproductive success; however, rapid growth can also have negative effects. Accelerated growth in juvenile life stages is associated with reduced longevity (Metcalf and Monaghan 2003). The link between rapid growth and the risk of death is well established because faster growth rates often require increased food intake, which in turn may increase incidences of exposure of the individual to predators (Gotthard 2000). Extrinsic factors that may change rapidly in the Murray River because of climate change or human activity may interact in complex ways. Populations of turtles that are on a fast growth trajectory through adaptation or increases in temperature, may also be more vulnerable to starvation during periods of food shortage (Blanckenhorn 2000), because their metabolism is adjusted to high rates of nutrients (Arendt 1997).

Regardless of an animal's life history strategy, there is a limited amount of energy available to it at any one time. From a theory of ageing view, if an organism grows at a faster rate, it does so at the expense of investment in maintenance and increases the potential of oxidative damage and telomere abrasion that are associated with respiration and cell division, accelerating cellular senescence (Houben *et al.* 2008). Faster development may also impair the quality of the structure, as observed in feathers (Dawson *et al.* 2000) and fish scales (Arendt *et al.* 2001). Cellular maintenance was tested in three short-lived and three long-lived Colubrid

species, and the long-lived species showed greater DNA repair capability (Robert *et al.* 2007, Bronikowski 2008). Similarly, the western terrestrial garter snake, *Thamnophis elegans*, has evolved into two separate ecotypes, representing both short-lived and long-lived life histories, and the long-lived group show greater DNA repair capabilities (Robert and Bronikowski 2010). These traits that have been linked to longevity would be expected to decrease in turtles if their life histories shifted towards short-lived strategies of faster growth and earlier maturity.

None of these theories have been tested in Australian species, which are amongst the longest-lived turtles in the world (Shine and Iverson 1995). Turtles and tortoises, in general, are long-lived vertebrates with some species being able to live in captivity more than 100 years, and have high adult survivorship in natural conditions (Gibbons and Semlitsch 1982). Unlike mammalian species, there has been no clear evidence to confirm these animals undergo any signs of senescence (Girondot and Garcia 1999). Negligible senescence refers to a few select animals, such as turtles, that do not display indicators of ageing. Indicators include measurable reductions in their reproductive capability or functional decline, or higher mortality in later life (Girondot and Garcia 1999). However, only two long-term studies of freshwater turtles have demonstrated negligible senescence (Congdon *et al.* 2001; Congdon *et al.* 2003). Cellular indicators of ageing in turtles are not consistent. Telomere lengths have not been researched amongst many turtle species, however in European freshwater turtles, *Emys orbicularis*, there appears to be no correlation with ageing (Girondot and Garcia 1999) yet in the loggerhead sea turtle, *Caretta caretta*, telomeres do appear to shorten with age (Hatase *et al.* 2008). Once a cell reaches the telomeres critical length and the telomeres become uncapped, the result is either senescence, apoptosis or activation of telomerase (Monaghan and Haussmann 2006). The association of telomere lengths and survival has also been seen in tree swallows, *Tachycineta bicolor*, where those individuals with longer telomere lengths survived more breeding seasons (Haussmann *et al.* 2005).

The highest rate of telomere loss occurs during juvenile stages (Hall *et al.* 2004). Animals that have accelerated growth during the juvenile stage usually have higher rates of telomere loss than then juveniles with normal growth (Hall *et al.* 2004). Regardless of whether telomeres shorten with age or during accelerated juvenile growth in turtles, the sheer length of them may in fact mean that they are immune to traditional indices of senescence. However, with a greater focus on growth, rather than maintenance, as turtles adapt to climate change and increased human activity on the Murray River, we may begin to see higher mortality rates and increased signs of ageing. Although more research is needed in this area, it may be that telomeres are long enough in turtles to circumvent the potential problem of immune dysfunction with age, as indicated by the fast growing and early maturing population of

C. picta in North America showing little decline in immune responses with age (Schwanz *et al.* 2011). They do however show some indication of ageing more rapidly than their slow growing conspecifics (Fig. 1). Fast growing hatchlings raised under common-garden experimental conditions have more Reactive Oxygen Species (ROS) in their blood after 1yr than slow growth hatchlings from other populations (Fig. 1). Another indication of the costs of accelerated growth is increased metabolism and cellular respiration. Mitochondria produce ROS as a by-product of cellular respiration (Droge 2002; Weinert and Timiras 2003) and when high ROS levels occur, mitochondrial function can be damaged, resulting in DNA damage and cell senescence.

Longevity is important to the reproductive strategy of turtles. There is a high mortality rate of juveniles but this is compensated by reproductive success throughout their lifespan, unlike mammals that progress to reproductive senescence. Long term studies of Blanding's turtle, *Emydoidea blandingii*, and painted turtles, *C. picta*, in Michigan have allowed aspects of field gerontology to be explored (Congdon *et al.* 2001; Congdon *et al.* 2003). Reproductive output and survivorship continues to increase in female *E. blandingii* (Congdon *et al.* 2001), which is similar to *C. picta*, however they are also able to continuously increase body size with age (Congdon *et al.* 2001; Congdon *et al.* 2003). *C. picta* in the fast

growing population in Illinois has adopted a different strategy. They mature up to four years earlier and at a smaller size than in Michigan, but increases in clutch size are not linear and asymptote within four years of the first year of reproduction (Spencer and Janzen 2009). Currently, female *E. macquarii* in Murray River display similar patterns to the long-living and later maturing populations of turtles in Michigan, where reproductive output increases linearly with body size and survival rates do not decline even in the oldest age/size classes (Spencer and Thompson 2005).

The impact of accelerated growth in Murray River turtles from decreases in water levels and elevated temperatures may see a major shift in the physiological and cellular functions that allow it to maintain its current life history strategies. Any life history changes have flow on affects for the ability of Murray River turtles to adapt, which will ultimately determine their survival. If Murray River turtles grow at faster rates as juveniles than they are currently, then a shift in their life history patterns may occur, so that maturity may occur at younger and at smaller sizes. This adaptive strategy is actually the process of increasing productivity of the population, but with long generation times, the resilience of these populations are likely to be tested because environmental conditions may change more rapidly than the internal population and physiological mechanisms of the turtles.

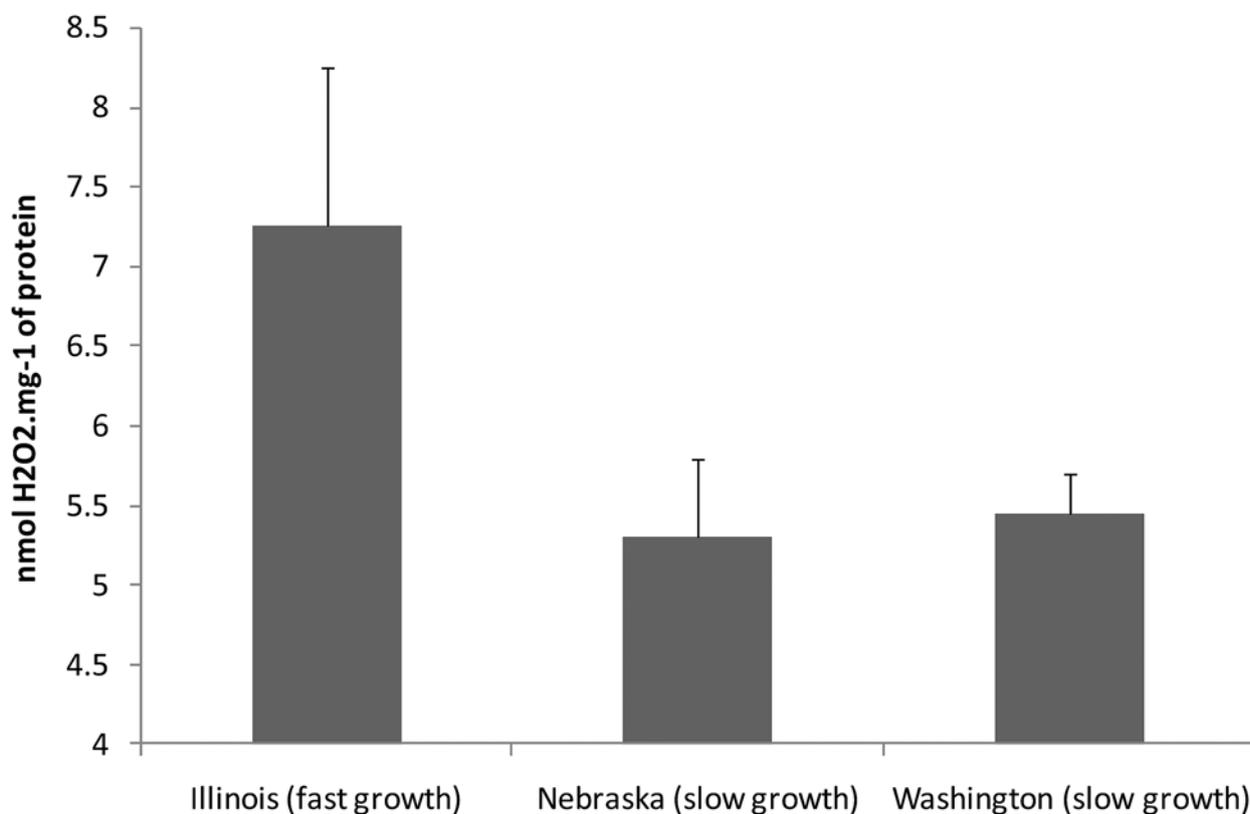


Figure 1. (a) H₂O₂ concentrations (±S.D) in blood of 1-yr-old painted turtles (USA) from a fast growing and human impacted population (IL) and from slow growing, pristine populations (NE and WA). Methods for obtaining H₂O₂ concentrations from blood are detailed in Robert *et al.* (2007). Reactive Oxygen Species (ROS)(free radicals), such as H₂O₂, attack proteins in DNA. Ageing results from damage by ROS (unpubl. Data Spencer R-J, Sparkman A and Bronikowski A.)

Managing For Climate Change

Resilience science is a relatively new branch of science that combines theoretical and applied aspects of ecology, physiology, evolution and molecular biology to understand the adaptive capacity of large long-lived species to climate change and human modification of riverine environments. Reducing vulnerability of our aquatic wildlife urgently requires the application of adaptation and mitigation options at appropriate scales. Their effectiveness depends on building community and national capacity to respond to changes and on mainstreaming climate change adaptation in policies regarding natural resource management. Turtles may represent a key species for managing aquatic vertebrates in the system. There are two major foci for managing the system for climate change and human activity. Firstly, it is critical to identify wetlands that are unlikely to dry over the next 50-100 years. These areas will be critical habitat for a range of species, including turtles. By identifying areas that will be critical habitat in the future, areas that are currently permanent, but are likely to dry, can also be identified and possible relocation strategies can be implemented- particularly in wetlands that are close to major roads. The development of environmental watering protocols is an initiative that will benefit both fish and turtles in the Murray River. The initiative improves understanding of how fish in floodplain wetlands have responded to environmental water conditions, such as levels and seasonality into a management-friendly decision support system. A predictive decision-support tool to support regional wetland management has been produced to allow adaptive management decisions for increasing drought and climate change from a local perspective (Goyder Institute for water research 2011). Maintaining the quality of these key wetlands is also critical. The use of the Murray-Darling Basin as an agricultural resource is unavoidable for Australia's economy, but a more holistic approach to the irrigation management and water diversions is needed (Kingsford 2000). The traditional conservation practices of minimising erosion and salinity are important initiatives in these key wetlands to maintain water quality and nesting habitat for turtles.

Secondly, management must also focus on enhancing the adaptive resilience of freshwater turtles and fish in the Murray River. Using the biology of the turtles is certainly the most cost effective strategy to enhance and maintain populations under increased stress. Nest predation is extremely high on Murray River turtles (Thompson 1986; Spencer 2002a), limiting the

potential resilience that may be established through density dependent selection for juvenile growth. Simply reducing the reliance on adult survival will increase the resilience of a population. *C. expansa* is in much smaller numbers than *E. macquarii* in the Murray River, but despite its vulnerable status, the higher juvenile recruitment of *C. expansa* makes it relatively more stable than *E. macquarii* (Spencer and Thompson 2005). Identifying wetlands, where foxes are reduced or removed, and they can become 'hubs' for recruitment throughout the River is an important strategy to maintain population resilience key. Predator proof fencing is currently being used in some areas of the Murray (Murray-Darling Basin Commission 2007) but this solution is not a widespread cost-effective solution. More broad-scale solutions may lie in the development of new toxins, such as para-aminopropiophenone (PAPP), and trials of Mechanical Ejectors (MEs) for predator control. The mode of action of PAPP is similar to carbon monoxide poisoning, but PAPP in high enough doses in production baits will kill bandicoots and goannas (Ballard *et al.* 2009), but used in MEs, it has the potential to provide continual fox control in sensitive areas on the Murray River where traditional 1080 baiting is problematic because of non-target issues. Fox baiting can achieve a significant reduction in nest predation (Spencer 2002a), but pulse fox baiting campaigns are largely ineffective at long-term control and are generally not cost-effective, particularly if management is not coordinated with all stakeholders across a landscape. MEs have been trialled for over 10 years in Australia and are now used by NSW National Parks and Wildlife Services (Marks and Wilson 2005).

Conclusions

Turtles are more than 200 million years old and they are survivors. However, humans over the last few hundred years have had a greater impact on their existence than any ice age or mass extinctions that occurred during the Cretaceous period. Climate change and changes in the aquatic habitat of the Murray River will impact turtles, but they are adaptable. Anthropogenic induced adaptation or evolution of long-lived organisms is becoming the norm, rather than the exception. Turtles have shown the capacity to live with, and even thrive in, areas where nest predation rates have been over 93% for at least 20 years (Thompson 1982; Spencer 2002a). Density appears the biological mechanisms by through which turtles can adapt and evolve, but the combined pressures of high mortality in more than one life stage because of habitat changes over the next 50-100 years may be enough to push them to the brink of extinction.

Acknowledgements

We would like to thank RZS (NSW) for the invitation to present at their annual forum. We would like to thank A. Bronikowski, F. Janzen and A. Sparkman for help with collection of painted turtles and laboratory

work conducted at Iowa State University. Research on this project is being conducted at the Hawkesbury campus of UWS and funded by a F. G. Swain Award.

References

- Arendt, J.D. 1997 'Adaptive intrinsic growth rates: An integration across taxa', *The Quarterly Review of Biology*, **72**, 149-77.
- Arendt, J.D., Wilson, D.S. and Stark, E. 2001 'Scale strength as a cost of rapid growth in sunfish', *Oikos*, **93**, 95-100.
- Ballard, G., Fleming, P. and Humphrys, S. 2009, 'Outcomes of a field trial of PAPP (Para-aminopropiophenone) for canid predator control', in WA Ruscoe (ed.), *22nd Australasian Wildlife Management Society Conference*, Napier, New Zealand.
- Beare, S. and Heaney, A. 2002, 'Climate change and water resources in the Murray Darling Basin, Australia', in *World Conference of Environmental and Resource Economists*, Monterey.
- Blanckenhorn, W.U. 2000 'The evolution of body size: What keeps organisms small?', *The Quarterly Review of Biology*, **75**, 385-407.
- Bowkett, A.E. 2009 'Recent Captive-Breeding Proposals and the Return of the Ark Concept to Global Species Conservation', *Conservation Biology*, **23**, 773-6.
- Bronikowski, A.M. 2008 'The evolution of aging phenotypes in snakes: A review and synthesis with new data', *Age*, **30**, 169-76.
- Chessman, B.C. 1988 'Habitat preferences of fresh-water turtles in the Murray Valley, Victoria and New-South-Wales', *Wildlife Research*, **15**, 485-91.
- Coltman, D.W. 2008 'Evolutionary rebound from selective harvesting', *Trends in Ecology & Evolution*, **23**, 117-8.
- Congdon, J.D., Nagle, R.D., Kinney, O.M. and van Loben Sels, R.C. 2001 'Hypotheses of aging in a long-lived vertebrate, Blanding's turtle (*Emydoidea blandingii*)', *Experimental Gerontology*, **36**, 813-27.
- Congdon, J.D., Nagle, R.D., Kinney, O.M., van Loben Sels, R.C., Quinter, T. and Tinkle, D.W. 2003 'Testing hypotheses of aging in long-lived painted turtles (*Chrysemys picta*)', *Experimental Gerontology*, **38**, 765-72.
- CSIRO and Australian Bureau of Meteorology 2007, *Climate change in Australia: technical report 2007*, New South Wales Government and Commonwealth Scientific and Industrial Research Organisation (CSIRO), Canberra.
- Dawson, A., Hinsley, S.A., Ferns, P.N., Bonser, R.H.C. and Eccleston, L. 2000 'Rate of moult affects feather quality: A mechanism linking current reproductive effort to future survival', *Proceedings: Biological Sciences*, **267**, 2093-8.
- Dodd, C.K. 2002, *North American box turtles: A natural history*, vol. 6, Animal Natural History Series, University of Oklahoma Press, Norman.
- Droge, W. 2002 'Free radicals in the physiological control of cell function', *Physiological Reviews*, **82**, 47-95.
- Ewert, M.A. and Nelson, C.E. 1991 'Sex determination in turtles: Diverse patterns and some possible adaptive values', *Copeia*, **1991**, 50-69.
- Ferguson, M.W.J. and Joanen, T. 1983 'Temperature-dependent sex determination in *Alligator mississippiensis*', *Journal of Zoology*, **200**, 143-77.
- Fordham, D.A., Georges, A. and Brook, B.W. 2007 'Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia', *Journal of Animal Ecology*, **76**, 1231-43.
- Galbraith, D.A., Bishop, C.A., Brooks, R.J., Simser, W.L. and Lampman, K.P. 1988 'Factors affecting the density of populations of common snapping turtles (*Chelydra serpentina serpentina*)', *Canadian Journal of Zoology*, **66**, 1233-40.
- Gibbons, J.W. and Semlitsch, R.D. 1982 'Survivorship and longevity of a long-lived vertebrate species: How long do turtles live?', *Journal of Animal Ecology*, **51**, 523-7.
- Girondot, M. and Garcia, J. 1999, 'Senescence and longevity in turtles: What telomeres tell us', in R Guyétant & C Miaud (eds), *9th Extraordinary Meeting of the Societas Europaea Herpetologica*, Université de Savoie. Le Bourget du Lac, France, pp. 133-7.
- Gotthard, K. 2000 'Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly', *Journal of Animal Ecology*, **69**, 896-902.
- Goyder Institute for water research 2011, *Environmental Water*, viewed 21/05/2011, <<http://goyderinstitute.org/programs/environment/index.php>>.
- Hall, M.E., Nasir, L., Daunt, E., Gault, E.A., Croxall, J.P., Wanless, S. and Monaghan, P. 2004 'Telomere loss in relation to age and early environment in long-lived birds', *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1571-6.
- Hatase, H., Sudo, R., Watanabe, K.K., Kasugai, T., Saito, T., Okamoto, H., Uchida, I. and Tsukamoto, K. 2008 'Shorter telomere length with age in the loggerhead turtle: A new hope for live sea turtle age estimation', *Genes and Genetic Systems*, **83**, 423-6.
- Hausmann, M.F., Winkler, D.W. and Vleck, C.M. 2005 'Longer telomeres associated with higher survival in birds', *Biology Letters*, **1**, 212-4.
- Houben, J.M.J., Moonen, H.J.J., van Schooten, E.J. and Hageman, G.J. 2008 'Telomere length assessment: Biomarker of chronic oxidative stress?', *Free Radical Biology and Medicine*, **44**, 235-46.
- Hulin, V., Delmas, V., Girondot, M., Godfrey, M.H. and Guillon, J.-M. 2009 'Temperature-dependent sex determination and global change: are some species at greater risk?', *Oecologia*, **160**, 493-506.
- Iverson, J.B. 1982 'Biomass in turtle populations: A neglected subject', *Oecologia*, **55**, 69-76.
- Janzen, E.J. 1994 'Climate change and temperature-dependent sex determination in reptiles', *Proceedings of the National Academy of Sciences*, **91**, 7487-90.
- Khan, S. 2008 'Managing climate risks in Australia: options for water policy and irrigation management', *Australian Journal of Experimental Agriculture*, **48**, 265-73.
- Kingsford, R.T. 2000 'Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia', *Austral Ecology*, **25**, 109-27.
- Kingsford, R.T., Walker, K.F., Lester, R.E., Young, W.J., Fairweather, P.G., Sammut, J. and Geddes, M.C. 2011 'A Ramsar wetland in crisis the Coorong, lower lakes and Murray mouth, Australia', *Marine and Freshwater Research*, **62**, 255-65.
- Marks, C.A. and Wilson, R. 2005 'Predicting mammalian target-specificity of the M-44 ejector in south-eastern Australia', *Wildlife Research*, **32**, 151-6.
- Metcalfe, N.B. and Monaghan, P. 2003 'Growth versus lifespan: perspectives from evolutionary ecology', *Experimental Gerontology*, **38**, 935-40.
- Michael, D. and Lindenmayer, D. 2010, *Reptiles of the NSW Murray catchment: a guide to their identification, ecology and conservation*, CSIRO Publishing, Collingwood, Vic.
- Miller, D., Summers, J. and Silber, S. 2004 'Environmental versus genetic sex determination: a possible factor in dinosaur extinction?', *Fertility and Sterility*, **81**, 954-64.

- Monaghan, P. and Haussmann, M.F. 2006 'Do telomere dynamics link lifestyle and lifespan?', *Trends in Ecology & Evolution*, **21**, 47-53.
- Morjan, C.L. 2003 'Variation in nesting patterns affecting nest temperatures in two populations of painted turtles (*Chrysemys picta*) with temperature-dependent sex determination', *Behavioral Ecology and Sociobiology*, **53**, 254-61.
- Murray-Darling Basin Commission 2007, 'Native Fish Strategy', in M Lintermans (ed.), *Proceedings of the Murray-Darling Basin Commission Native Fish Strategy Forum 2007*.
- Near, T.J., Meylan, P.A. and Shaffer, H.B. 2005 'Assessing concordance of fossil calibration points in molecular clock studies: An example using turtles', *The American Naturalist*, **165**, 137-46.
- Quiggin, J. 2001 'Environmental economics and the Murray-Darling river system', *Australian Journal of Agricultural and Resource Economics*, **45**, 67-94.
- Robert, K.A. and Bronikowski, A.M. 2010 'Evolution of senescence in nature: physiological evolution in populations of garter snake with divergent life histories', *The American Naturalist*, **175**, 147-59.
- Robert, K.A., Brunet-Rossini, A. and Bronikowski, A.M. 2007 'Testing the 'free radical theory of aging' hypothesis: physiological differences in long-lived and short-lived colubrid snakes', *Aging Cell*, **6**, 395-404.
- Schwanz, L., Warner, D.A., McGaugh, S., Terlizzi, R.D. and Bronikowski, A. 2011 'State-dependent physiological maintenance in a long-lived ectotherm, the painted turtle (*Chrysemys picta*)', *The Journal of Experimental Biology*, **214**, 88-97.
- Shine, R. and Iverson, J.B. 1995 'Patterns of survival, growth and maturation in turtles', *Oikos*, **72**, 343-8.
- Spencer, R.-J. 2002a 'Experimentally testing nest site selection: Fitness trade-offs and predation risk in turtles', *Ecology*, **83**, 2136-44.
- Spencer, R.-J. 2002b 'Growth patterns of two widely distributed freshwater turtles and a comparison of common methods used to estimate age', *Australian Journal of Zoology*, **50**, 477-90.
- Spencer, R.-J. and Janzen, E.J. 2010 'Demographic consequences of adaptive growth and the ramifications for conservation of long-lived organisms', *Biological Conservation*, **143**, 1951-9.
- Spencer, R.-J., Janzen, E.J. and Thompson, M.B. 2006 'Counterintuitive density-dependent growth in a long-lived vertebrate after removal of nest predators', *Ecology*, **87**, 3109-18.
- Spencer, R.-J. and Thompson, M.B. 2005 'Experimental analysis of the impact of foxes on freshwater turtle populations', *Conservation Biology*, **19**, 845-54.
- Spencer, R.-J., Thompson, M.B. and Hume, I.D. 1998 'The diet and digestive energetics of an Australian short-necked turtle, *Emydura macquarii*', *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*, **121**, 341-9.
- Swain, D.P., Sinclair, A.F. and Mark Hanson, J. 2007 'Evolutionary response to size-selective mortality in an exploited fish population', *Proceedings. Biological sciences / The Royal Society*, **274**, 1015-22.
- Thompson, M.B. 1982 'A marking system for tortoises in use in South Australia', *South Australian Naturalist*, **57**, 33-4.
- Thompson, M.B. 1983 'Populations of the Murray River tortoise, *Emydura* (Chelodina): the effect of egg predation by the red fox, *Vulpes vulpes*', *Australian Wildlife Research*, **10**, 363-71.
- Thompson, M.B. 1986, *River Murray Wetlands. Their Characteristics, Significance and Management.*, South Australian Department of Environment and Planning, Adelaide.
- Thompson, M.B. 1993, 'Hypothetical considerations of the biomass of chelid tortoises in the River Murray and the possible influences of predation by introduced fox', in D Lunney & D Ayes (eds), *Herpetology in Australia*, Surrey Beatty and Sons, Sydney, pp. 219-24.
- Turtle Conservation Fund 2002, *A Global Action Plan for Conservation of Tortoises and Freshwater Turtles. Strategy and Funding Prospectus 2002-2007*, Conservation International and Chelonian Research Foundation, Washington, DC.
- Wei, Y., Langford, J., Willett, I.R., Barlow, S. and Lyle, C. 2011 'Is irrigated agriculture in the Murray Darling Basin well prepared to deal with reductions in water availability?', *Global Environmental Change, In Press, Corrected Proof*.
- Weinert, B.T. and Timiras, P.S. 2003 'Invited review: Theories of aging', *Journal of Applied Physiology*, **95**, 1706-16.
- Wilson, C. and Tisdell, C. 2001 'Sea turtles as a non-consumptive tourism resource especially in Australia', *Tourism Management*, **22**, 279-88.

APPENDIX I



Pond set-up of experiment at UWS Hawkesbury campus. Photo, F.Loudon.

APPENDIX I



Emydura macquarii hatching.
Photo, F. Loudon.



Emydura macquarii hatchling on rock.
Photo, F. Loudon.



Area of Murray River that *Emydura macquarii* in this study were caught.
Photo, F. Loudon.

APPENDIX I



Hatchling *Emydura macquarii* in a pond at UWS Hawkesbury campus. Photo, F. Loudon.



Two turtles released last year, showing the size difference in hatchlings of similar ages (within 2 weeks of each other) kept in high population density. Photo, R. Spencer