

How Much Long-Term Data Are Required to Effectively Manage A Wide-Spread Freshwater Turtle?

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ABSTRACT

Freshwater turtle populations are globally threatened by many factors. Complicating matters, their longevity requires long-term monitoring on the scale of decades to assess changes in population size, yet few long-term studies exist. Documenting population estimates and trends is essential for identifying and conserving imperilled populations, however, the impacts of many current threats may render populations endangered well before declines become apparent. By that stage, population recovery may not be possible, thus assessing population level impacts of potential threats may provide a direct measure of risks of population extinction. Australian turtles face major threats of mortality from invasive species, vehicles, disease and declining water quality. Even Australia's most abundant and widespread species has declined by up to 91% in some populations. Here I use population models to assess the impacts of threats to multiple life history stages of an Australia turtle. This study clearly demonstrates that *Chelodina longicollis*, Australia's most widespread turtle (1) is resilient to high levels of nest predation for sustained periods, (2) requires only periodic levels of reduced nest predation and pulse recruitment to maintain population viability and (3) low levels of adult mortality can drive populations to extinction. Turtle populations require pulse recruitment (i.e. nest predation rates declining to <35% every ten years) and monitoring of nest predation rates for 5-6 years to determine whether nest predation level profiles are extreme. However, if terrestrial mortality of adult turtles occurs, then the risk of extinction is high regardless of nest predation levels. Monitoring protocols to assess nest predation and adult mortality rates are not widely developed for freshwater turtles and here I develop a management plan that employs Citizen Science and standardised on-ground protocols to assess levels of threats at the population level. Standardised protocols and involvement of the public and community groups creates a network for broad-scale assessment and management of a species. Although threats can be identified and easily quantified and long-term data has demonstrated the extent of the decline of freshwater turtle populations in southern Australia, solutions to minimise risks of extinction need to be developed and fast-tracked before turtles throughout Australia become critically endangered.

Key words: Turtle, *Chelodina longicollis*, Management Plan, Population Modelling, Foxes, Invasive Species, Road Death

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Introduction

Freshwater turtle populations throughout the world are threatened by many factors, including habitat degradation and destruction, exploitation, pollution, disease, and invasive animals (Chessman 2011, Ernst *et al.* 1994; Buhlmann & Gibbons 1997; Jacobson 1997; van Dijk *et al.* 2000; Moll & Moll 2004). The longevity of turtles requires long-term monitoring on the scale of decades to assess changes in population size, yet relatively few long-term studies exist (e.g. Chessman 2011, Congdon *et al.* 1993, 1994; Foscari & Brooks 1997; Moll & Moll 2004). Documenting population estimates and trends is essential for identifying and conserving imperilled populations (Gibbons *et al.* 2000), however understanding population level impacts of potential threats may provide a direct measure of risks of population extinction.

Australian freshwater turtles currently face many threats that permeate every life history stage, from egg to adult. The life history of turtles involves high but fluctuating

rates of egg and juvenile mortality, balanced by extreme iteroparity (i.e. long-lived, highly fecund), in which threats to adult survival are low. Humans have impacted this selective regime at several life history stages. Mortality of eggs and young has increased, primarily because of predation by foxes (Thompson 1983), and adult mortality is increasing (Spencer and Thompson 2005). Adult turtles frequently become victims of road kill or are killed by foxes as they emerge to nest or disperse throughout wetlands (Spencer and Thompson 2005). Turtles are also struck by boats,

drowned in fishing nets or in irrigation pumps, and killed by fishers. Mortality rates in the egg stage have increased, with over 93% of nests on the River Murray destroyed by European foxes (*Vulpes vulpes*) (Thompson 1983; Spencer 2002). As a result, turtles in the River Murray appear at risk of extinction and are in serious decline, with abundances 69-91% lower than 40 years ago (Chessman 2011). Large biomasses of turtles (100K tonnes- Thompson 1993) are threatened by chronic reproductive failure, exotic predators, disease, habitat modification and habitat loss over past decades. Impacts reached a climax during the recent 'millennium drought' with reports of mass turtle mortality, as historically permanent wetlands dried- a condition that may become commonplace under predictions of climate change (Roe and Georges, 2010). Salinity rose in the lower lakes and fringing wetlands of South Australia, and many turtles perished, as growths of estuarine tubeworms established on their shells (Bower *et al.* 2012). Potential for post-drought recovery is limited by ongoing threats and capacity for populations to increase.

Although long-term monitoring is required to confirm population declines of freshwater turtles, population modelling of potential threats may allow for early identification of at risk species or populations. Such modelling can also aid the development and implementation of harm mitigation strategies to circumvent long-term declines and risks of extinction because turtle longevity masks the extent of threats, as adults persist with extreme mortality and reduced recruitment for decades before a decline becomes evident. Here I assess the impacts, or risks of extinction from current threats to many Australian turtles and develop protocols that can employ easy to implement Citizen Science techniques to monitor impacts.

Methods

I used the Eastern long-necked turtle (*Chelodina longicollis*) as the model species for this study. *Chelodina longicollis* is the most widespread freshwater turtle in Australia, with an extensive range across eastern Australia (Cann and Sadlier 2017). Its range broadly overlaps human populated areas and includes the capital cities of Brisbane, Melbourne, Canberra, Adelaide and Sydney (Cann and Sadlier 2017; Kennett *et al.* 2009). *Chelodina longicollis* occupies a wide range of habitats, such as shallow ephemeral swamps, farm dams and flowing rivers (Chessman 1988). Their estimated population densities vary between 26 and 400 turtles ha⁻¹ (Parmenter 1976; Kennett *et al.* 2009, Ferronato 2015). Their lifespan is not known, but they are slow growing and may live more than 100 years (Parmenter 1976; Thompson 1993). Females emerge from the water to oviposit one clutch annually of 10-20 eggs (Parmenter 1976; Thompson 1993; Vestjens 1969) and both sexes frequently migrate overland among

water bodies to exploit ephemeral swamps (Kennett and Georges 1990; Stott 1987). They are carnivorous, consuming primarily aquatic insects and carrion (Chessman 1988). Nest predation rates are extremely high in south-eastern Australia, with >90% of nests destroyed each year (Thompson 1983; Spencer 2002; Spencer *et al.* 2016). Based on our model parameters, an initial population size 1000 produces a stable stage trappable population of 250 turtles. Thus we set an upper carrying capacity of 2000 individuals to reflect the upper limits of the trappable population in the wild (Spencer *et al.* 2017).

With nest predation rates high, I created a range of nest predation rate scenarios where the mean nest predation rate varies, but in any given year, nest predation rates could be 100%. Five nest predation regimes were created 1) 95±5% 2) 90±10% 3) 85±15% 4) 75±25% and 5) 50±50%. Firstly based on these regimes, I generated random annual nest predation rates over 1000 years to determine number of years and consecutive years that nest predation rates were over 90% for each regime. This is to help guide management to determine monitoring regimes and assess impact. Using these same nest predation regimes, I constructed matrix population projection models (PopTools; Hood 2010) and used Vortex 10.0 (Lacy 2000) to assess population viability analysis of current *Chelodina longicollis* populations. I modelled a range of management scenarios where (1) nest predation rates were set at those defined regimes (2) nest predation rates were set at those defined regimes and 2% of the adult female population were harvested each year (~1% of the adult population) (3) nest predation rates were set at 95±5% but every 5, 10, or 20 years reduced to 80% to represent small levels of pulse recruitment and (4) nest predation rates were set at 95±5 % but reduced to 75%, 60%, and 35% every ten years to represent varying magnitudes of pulse recruitment. (e.g., Spencer *et al.* 2016). The remaining life history parameters for the population models were from Spencer *et al.* (2017): (1) age at maturity was set at 10y for females and 6y for males (2) Juvenile survival was size dependent and ranged from 50%-90% (±10%) and adult survival was set at 95% (±5%) per annum and (3) Adult females produced a single clutch of up to 20 eggs (15±5) and turtles could live up to 70y. No random perturbations or extreme environmental events were included in the models. These events would occur naturally and increase rates of extinction.

Results

Recruitment and Nest Predation

In any random year over 1000 years, nest predation rates greater 90% are common at all levels of predation that I modelled (Fig. 1). However, only the 85±15% and 90±10% nest predation regimes yielded nest predation rates greater than 90% for more than five consecutive years (Fig. 1).

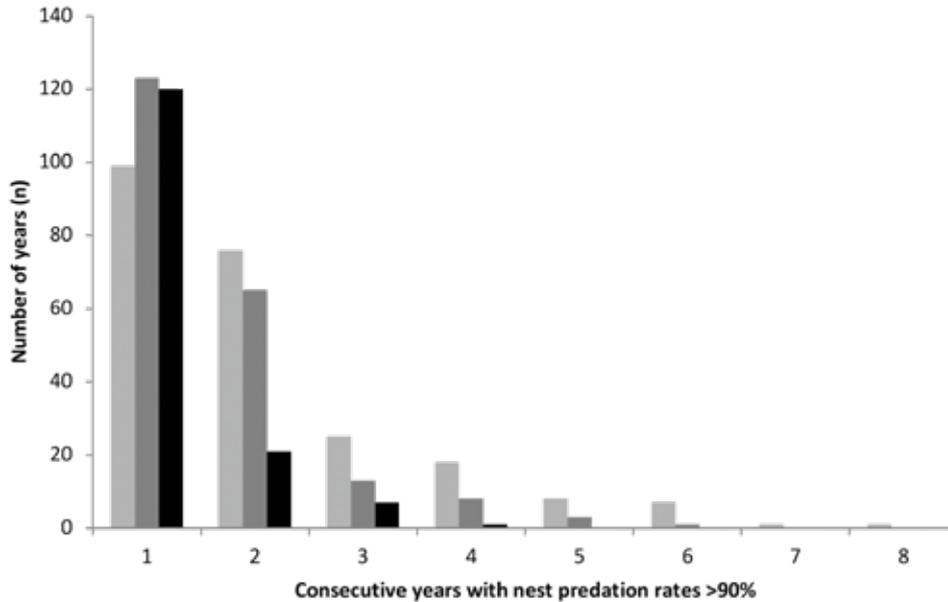


Fig. 1. Histogram (Count) of consecutive years (over 1000 years) where nest predation rates were >90% when nest predation rates are randomly set within the following regimes- 90±10% (light grey), 85±15% (dark grey), and 75±25% (black).

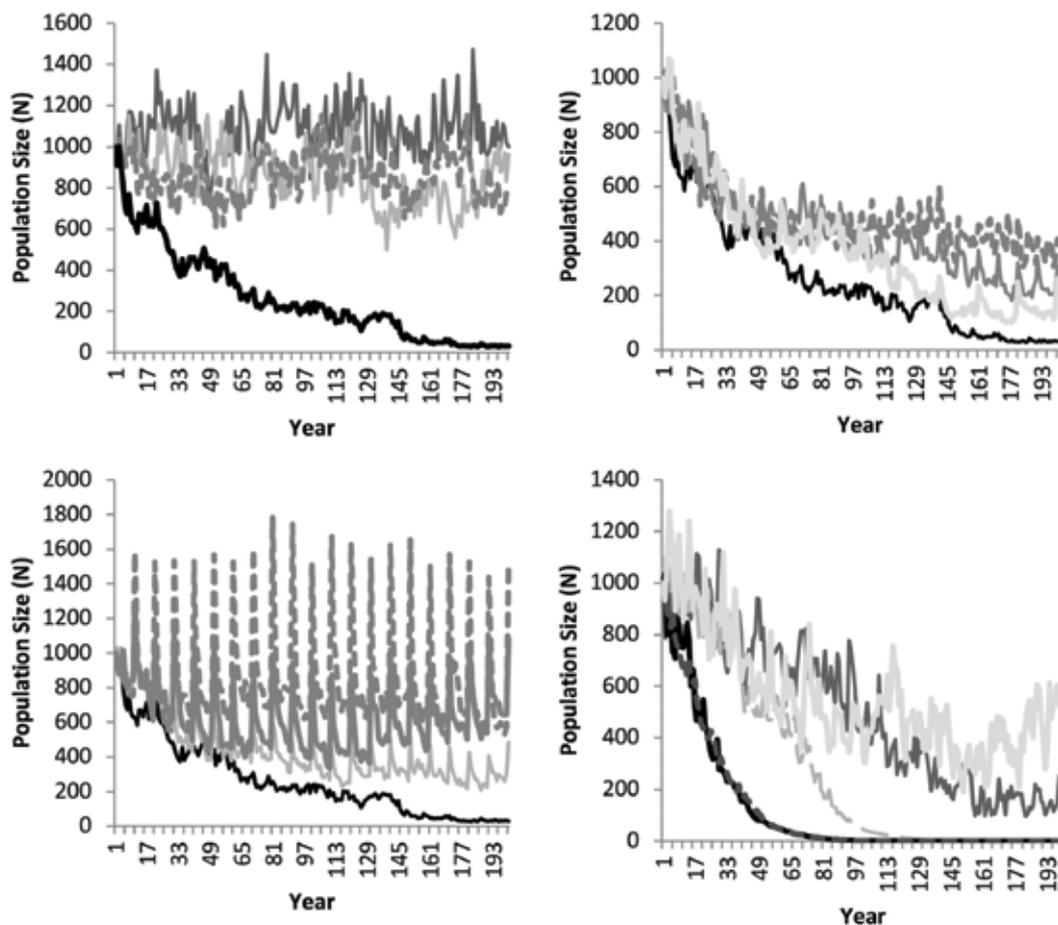


Fig. 2. (a) Projected population size based on nest predation rates of 75±25 % (dark grey solid line), 85±15% (light grey solid line), 90±10% (dashed dark grey line) and 95±5% (solid black line) (b) Projected population size based on nest predation rates of 95±5 % (solid black line), with predation rates declining to 80% every five years (dashed dark grey line), ten years (dark grey solid line), and 20 years (light grey solid line) (c) Projected population size based on nest predation rates of 95±5 % (solid black line), with predation rates declining to 75% every ten years (light grey solid line), 60% (dark grey solid line), and 35% (grey dashed line) (d) Projected population size based on nest predation rates of 50±50% (light grey solid line) 75±25 % (dark grey solid line), 85±15% (light grey dashed line), 90±10% (dashed dark grey line) and 95±5% (solid black line), including a harvest rate of 2% of the adult female population per year.

Table 1. Growth rates and probabilities of extinction based on a range of nest predation rates

Nest Predation Rate (%)	Deterministic growth rate (r)	Stochastic growth rate (r)	Probability of Extinction
75±25	0.061	0.0539	0
85±15	0.0348	0.0225	0
90±10	0.0164	0.0116	0
95±5	-0.0106	-0.021	0.4

Table 2. Population growth rates and probabilities of extinction based on high nest predation rates where nest predation rates decline to 80% one year in 5, 10, and 20.

Nest Predation Rate (%)	Deterministic growth rate (r)	Stochastic growth rate (r)	Probability of Extinction
95±5 reduction every 5 years	-0.0106	-0.0023	0
95±5 reduction every 10 years	-0.0106	-0.0048	0
95±5 reduction every 20 years	-0.0106	-0.0068	0
95±5 no reduction	-0.0106	-0.021	0.4

Turtle populations can absorb high levels of nest predation and maintain population growth (Fig. 2(a)). Once nest predation rates reach 95±5%, the risk of extinction increases (Table 1). Slight reductions in nest predation rate (from >90% to 80%) every 5-20 years reduces the risk of extinction over 200 years (Table 2), but population growth rates remain negative (Fig. 2(b)). One year of ten where nest predation rates decline to <60% produces enough recruitment to maintain the population (Fig. 2(c)) and eliminate the risk of extinction (Table 3).

Impacts of Increased Adult Mortality

When less than 1% of the adult population (~2% of

adult females) are harvested from the population each year, the risk of extinction remains high (>60%) and only nest predation rates of <75±25% in our models leads to positive deterministic growth rates (Table 4), although stochastic growth rates can be negative and easily lead to population extinction (Fig. 2(d)).

Discussion

Australian freshwater turtles are at significant risks of extinction from a range of factors including reduced juvenile recruitment from fox predation and increased mortality on adults through road deaths, predation and

Table 3. Population growth rates and probabilities of extinction based on high nest predation rates where nest predation rates decline to 75%, 60% and 35% every ten years.

Nest Predation Rate (%)	Deterministic growth rate (r)	Stochastic growth rate (r)	Probability of Extinction
95±5 reduction to 75% every 10 years	-0.0106	-0.0004	0
95±5 reduction to 60% every 10 years	-0.0106	0.004	0
95±5 reduction to 35% every 10 years	-0.0106	0.0172	0
95±5 no reduction	-0.0106	-0.021	0.4

Table 4. Growth rates and probabilities of extinction based on a range of nest predation rates, including a harvest rate of 2% of the adult female population per year.

Nest Predation Rate (%)	Deterministic growth rate (r)	Stochastic growth rate (r)	Probability of Extinction
50±50	0.1016	0.032	0.6
75±25	0.061	-0.0008	0.8
85±15	0.0348	-0.0174	1
90±10	0.0164	-0.0497	1
95±5	-0.0106	-0.0526	1

reduced habitat quality. This study clearly demonstrates that *Chelodina longicollis*, Australia's most widespread turtle (1) is resilient to high levels of nest predation for sustained periods, (2) requires only periodic levels of reduced nest predation and pulse recruitment to maintain population viability and (3) low levels of adult mortality can drive populations to extinction. The implications for management are significant. Turtle populations require pulse recruitment (i.e. nest predation rates declining to <35% every ten years) and monitoring of nest predation rates for 5-6 years to determine whether nest predation level profiles are extreme. However, if even modest rates of terrestrial mortality of adult turtles occurs, then the risk of extinction is high regardless of nest predation levels.

Monitoring protocols to assess nest predation and adult mortality rates are not developed for freshwater turtles and here developing simple and effective protocols for basic population assessments for management agencies, community groups and the general public. Monitoring adult mortality is relatively simple, with regular and random surveys on roads and around wetlands recovering turtle remains. Road kill around wetlands is common and the Citizen Science tool, TurtleSAT utilises the GPS function of mobile phones and Google Maps™ to accurately record turtle activity and sightings. Data can be recorded with an easy to use interface through an iOS™ and Android™ app or a website (TurtleSAT.org.au), which allows for broad-scale identification of mortality hotspots (Spencer *et al.* 2017) and patterns of activity (Santori *et al.* 2017). Although these surveys may not identify rates of mortality, zero adult mortality tolerance levels should be implemented by management because even low levels of increased adult mortality exposes populations to increased risks of extinction. Apart from road mortality, foxes are also a major source of adult mortality (Fig. 3). Foxes intercept female turtles as they emerge from the water to nest or migrate over land. The signs of predation by foxes or dogs are easy to identify. Carcasses can be relocated close to dens and multiple carcasses are often found around dens. Other signs of fox or dog predation include carcasses with legs and heads removed or snapped and teeth marks and chips out of the plastron (Fig. 3).

Quantifying nest predation rates using turtle nests is virtually impossible unless turtles are observed nesting. Nesting of many Australian species occurs during rain (Bowen *et al.* 2005) and once a turtle returns to the water, nests are visually well camouflaged, however, they are easily discovered by foxes, which destroy more than 93% of nests each year (Thompson 1983, Spencer 2002, Spencer *et al.* 2017). Nests are often depredated within minutes or hours of oviposition and become easily identifiable, with a hole, obvious diggings, and egg shell deposited on the surface. This allows for easy

identification and mapping of nesting areas around each population, because egg shells can remain in the area for several months. Nesting areas are commonly re-used by turtles each year (Petrov *et al.* 2017) and TurtleSAT allows for easy recording and mapping of nesting activity at a population (Fig. 3). However, to quantify levels of nest predation, the creation of standardised artificial nest protocols will aid year to year monitoring and broad-scale assessments of the status of turtle populations, as well as, allow for easy monitoring of the impacts of fox control management. The numerical response of fox predation on turtle nests is not linear and very low numbers of foxes can cause as much damage as high numbers of foxes in an area (Spencer *et al.* 2016, Spencer *et al.* 2017), thus standard indices for assessing success of fox management programs (eg. Bait uptake or reduction in fox activity) may not reflect reductions in nest predation. The creation of a known number of artificial nest plots to monitor the fate of nests that can be created out of commercially purchased infertile chicken or quail eggs (see Spencer *et al.* 2017) and placed at common nesting areas of a population. This method is a cost-effective and is simple enough for incorporating into activities of non-experts, such as the general public, community groups and land management agencies. Artificial nest plots should be placed near all identified turtle nesting areas, but trials should avoid peak nesting times or when high densities of turtle nests may be underground. Standardised monitoring over 6 years determines the nest predation profile level and is directly comparable to similar trial in other regions, which can evaluate the extent of the problem. Artificial nest trials, before and after any fox management programs in an area also aids in evaluating the success of the control program.

Managing for high levels of fox predation and low adult mortality is problematic because traditional fox management rarely reduces activity to low enough levels to reduce nest predation rates in an area (Spencer *et al.* 2017). If high mortality rates due to foxes is isolated, fencing nesting beaches or targeted shooting may reduce both nest and adult predation rates, but broadscale management is problematic. Similarly, the impacts of roads can be especially significant for terrestrial species that inhabit water bodies, such as freshwater turtles (Hamer *et al.* 2015). Many freshwater turtles undertake migrations on land to find suitable nesting grounds, disperse to new wetlands for foraging and reproduction, or to escape drying water bodies (Roe and Georges 2008; Steen *et al.* 2006). Because of these movements, freshwater turtles around the world are hit by vehicles. Permanent or temporary road signs during nesting season around wetlands with high adult mortality is a common way to alert drivers, however barriers to redirect the movement of turtles at road access points could also be considered. The installation of roadway mitigation measures is becoming increasingly common and the construction of ecopassages, or



Fig. 3. Top photos show Broad-shelled turtle (*Chelodina expansa*) road mortality during nesting season. Middle photos show nests depredated by foxes. Diggings and egg shells remain and often footprints or scats are left by foxes. Bottom photo includes TurtleSAT data overlaid on a map. Gold dots are depredated nests and other coloured dots are locations of where turtle carcasses were found. Photo credits TurtleSAT and Turtles Australia.

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retro-fitting existing ecopassages under existing roads, particularly under multi-lane highways where vehicles are travelling at high speed and lane barriers are often present, may reduce turtle road mortality. However, it is vital to implement and design mitigation measures with the biology and behaviour of the target species in mind (Baxter-Gilbert *et al.* 2015).

Many of Australia's freshwater turtles are on the precipice of extinction and while there are methods to effectively assess the impact of current threats, there are no clear methods to mitigate them. Where broad-scale management of threats is problematic, Spencer *et al.* (2017) advocate bypassing direct management of the threat and focussing on mitigating impacts of external mortality through harnessing the reproductive potential of freshwater turtles. Their longevity, combined with high annual reproductive output (Cann and Sadler 2017), allows for the creation of harvest populations or headstarting programs (Fig. 4), whereby single populations can service many populations at a regional level to mitigate the impacts of high external mortality (Spencer *et al.* 2017). Protecting or creating islands for turtle to nest on in lakes or lagoons may also provide an effective solution for mitigating the impacts of foxes.

Strong consideration to the genetic consequences of such manipulations must also be assessed. Although long-term data have demonstrated the extent of the decline of freshwater turtle populations in southern Australia (Chessman 2011), solutions to minimise risks of extinction need to be fast-tracked before species become critically endangered. The longevity of turtles, combined with external threats to multiple life history stages, means that ageing populations with minimal levels of juvenile recruitment became endangered well before any declines in population size.

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Fig. 4. (a) Murray Short-Necked Turtles (*Emydura macquarii*) part of a headstarting program in Lake Bonney in South Australia. (b) Juvenile Eastern Long-Neck Turtle (*Chelodina longicollis*) released into the Hawkesbury (NSW), which is rare in most populations because of egg predation by foxes. Photos by Ricky Spencer.

References

- Bowen, K.D, Spencer, R.J and Janzen, F.J. 2005. A comparative study of environmental factors that affect nesting in Australian and North American freshwater turtles., *Journal of Zoology London*, 267: 397-404.
- Bower, D.S, Scheltinga, D.M., Clulow, S., Clulow, J., Franklin, C.E., Georges, A. 2016. Salinity tolerances of two Australian freshwater turtles, *Chelodina expansa* and *Emydura macquarii* (Testudinata: Chelidae). *Conservation Physiology*. 4:cow042. doi:10.1093/conphys/cow042.
- Buhlmann, K. A., & J. W. Gibbons. 1997. Imperilled aquatic reptiles of the southeastern United States: historical review and current conservation status. Pp. 201–232 in *Aquatic Fauna in Peril: The Southeastern Perspective, Special Publication 1*. Edited by G.W. Benz and D.E. Collins. Aquatic Research Institute, Lenz Design and Communications.
- Cann J. and Sadler R. 2017. *Freshwater Turtles of Australia*. CSIRO Publishing. Canberra.

- Chessman, B.C.** 1988. 'Habitat preferences of freshwater turtles in the Murray Valley, Victorian and New South Wales'. *Australian Wildlife Research* 15: 485-491.
- Chessman, B.C.** 2011. Declines of freshwater turtles associated with climatic drying in Australia's Murray-Darling Basin. *Wildlife Research* 38:664–671.
- Congdon, J. D., A. E. Dunham, and van Loben Sels R. C.** 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7:826–833.
- Ernst, C. H., J. E. Lovich, and Barbour R. W.** 1994. *Turtles of the United States and Canada*. Smithsonian Institution Press, Washington.
- Ferronato, B.O, Roe, J.H, and Georges, A.** 2014. Reptile bycatch in a pest-exclusion fence established for wildlife reintroductions. *J. Nature Conservation* 22: 577-85.
- Foscarini, D. A., & Brooks R. J.** 1997. A proposal to standardize data collection and implications for management of the wood turtle, *Clemmys insculpta*, and other freshwater turtles in Ontario, Canada. Pp. 203–209 in Proceedings: *Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*. Edited by J. Van Abbema. New York Turtle and Tortoise Society, New York.
- Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and Winne C. T.** 2000. The global decline of reptiles, déjà vu amphibians *BioScience*. 50:653– 666.
- Hamer, A.J., Harrison, L.J., Stokeld, D.** 2016. Road density and wetland context alter population structure of a freshwater turtle. *Austral Ecology* 41: 53–64.
- Jacobson, E. R.** 1997. Diseases in wild populations of turtles and tortoises: the chelonian charisma vs. coincidence conundrum. Pp 87–90 in Proceedings: *Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*. Edited by J. Van Abbema. New York Turtle and Tortoise Society, New York.
- Kennett R and Georges A.** 1990. Habitat utilisation and its relationship to growth and reproduction of the eastern long-necked turtle *Chelodina longicollis* (Testudinata: Chelidae), from Australia. *Herpetologica*. 46: 22-33.
- Kennett R, Roe J, Hodges K and Georges A.** 2009. *Chelodina longicollis* (Shaw 1784)- eastern long-necked turtle, common long-necked turtle, common snake-necked turtle. *Chelonian Research Monographs* 5: 031.1-031.8.
- Kurz, D., Straley, K., and Degregorio, B.** 2011. Out-foxing the red fox: How best to protect the nests of the Endangered loggerhead marine turtle *Caretta caretta* from mammalian predation? *Oryx*. 46: 223-228.
- Lacy, R.C.** 2000. Structure of the VORTEX simulation model for population viability analysis. *Ecological Bulletins* 48:191-203.
- Moll, D., and Moll E.O.** 2004. *The Ecology, Exploitation, and Conservation of River Turtles*. Oxford University Press, New York.
- Parmenter, C.J.** 1976. The natural history of the Australian freshwater turtle, *Chelodina longicollis* (Shaw) (Testudina, Chelidae). Doctor of Philosophy, The University of New England, Armidale, NSW.
- Petrov, K.A, Stricker, H., Van Dyke, J.U.V, Stockfeld, G., West, P, Spencer, R-J.** 2017. Nesting Ecology of the Broad-shelled Turtle (*Chelodina expansa*). *Australian Journal of Zoology*. In press
- Santori, C., Spencer, R-J., Van Dyke, J.U.V, Thompson, M.B.** 2017. Using citizen-collected observations to assess turtle road kill along the Murray River, Australia. *Australian Journal of Zoology*. In press.
- Spencer, R-J.** 2002. Experimentally testing nest site selection: fitness trade-offs and predation risk in turtles. *Ecology* 83: 2136-2144.
- Spencer, R-J., and Thompson, M.B.** 2005. Experimental analysis of the impact of foxes on freshwater turtle populations *Conservation Biology* 19:845–854.
- Spencer, R-J., Van Dyke, J.U.V and Thompson, M.B.** 2016. The ethological trap: functional and numerical responses of highly efficient invasive predators driving prey extinctions. *Ecological Applications* 26: 1969–1983.
- Spencer, R.J., Van Dyke, J.U. and Thompson, M. B.** 2017. Critically evaluating best management practices for preventing freshwater turtle extinctions. *Conservation Biology*. Accepted Author Manuscript. doi:10.1111/cobi.12930.
- Thompson, M.B.** 1983. Populations of Murray river tortoise, *Emydura* (*Chelodina*): the effect of egg predation by the red fox, *Vulpes vulpes*. *Wildlife Research* 10: 363–371.
- Thompson, M.B.** 1993. Hypothetical considerations of the biomass of chelid tortoises in the River Murray and the possible influence of predation by introduced foxes. In: *Herpetology in Australia. A diverse discipline*. Edited by Lunney, D. & D. Ayres. Royal Zoological Society of NSW, Mosman, N.S.W. pp. 219-224.
- van Dijk, P. P., Stuart B. L., & Rhodin, A. G. J.** 2000. Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. Chelonian Research Monographs No. 2. New York Turtle and Tortoise Society, New York.
- Vestjens W.** 1969. Nesting, egg-laying and hatching of the snake-necked tortoise at Canberra, A.C.T. *Australian Zoologist* 15: 141-149.