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Author:
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Publication details:
Pacific Conservation Biology
v. 28
Chapter No. 6
pp. 462 - 471
1038-2097 (ISSN); 2204-4604 (ISSN)

Publication Date:
2021-01-01

Publisher DOI:
https://doi.org/10.1071/PC21058

CSIRO PUBLISHING

REVIEW
https://doi.org/10.1071/PC21058

PACIFIC CONSERVATION BIOLOGY

Introduced red foxes (*Vulpes vulpes*) driving Australian freshwater turtles to extinction? A critical evaluation of the evidence

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Handling Editor:
Mike Calver

Received: 1 September 2021
Accepted: 21 November 2021
Published: 14 December 2021

Cite this:
Chessman BC (2021)
Pacific Conservation Biology
doi:10.1071/PC21058

ABSTRACT

It has been asserted that introduced red foxes (*Vulpes vulpes*) destroy ~95% of nests of freshwater turtles in south-eastern Australia, are more efficient predators of freshwater turtle nests than Australian native predators, and are driving Australian freshwater turtle species to extinction. Available information was reviewed and analysed to test these assertions. Nest predation rates for all predators including foxes averaged 70% across Australia and 76% for south-eastern Australia compared to 72% for North America where freshwater turtles co-exist with many native predators, including foxes. Predation rates on Australian freshwater turtle nests did not differ significantly where foxes were included in the identified nest predators and where they were not, but sample sizes were very small. Evidence was lacking of foxes being the primary driver of population declines of Australian freshwater turtles, and some turtle populations are stable or increasing despite exposure to fox predation. Australian native species can be effective nest predators, and their role has probably been usurped by foxes to some degree. Where research shows that increased recruitment is necessary to conserve Australian freshwater turtle populations, strategies such as electric fencing of nesting beaches, nest protection cages and *ex situ* incubation of turtle eggs will probably be more cost-effective than efforts to reduce fox numbers. Further research is also needed to better understand the biological and environmental factors that regulate nest predation rates.

Keywords: Australia, extinction, freshwater, invasive species, nest, predation, turtle, *Vulpes vulpes*.

Introduction

More than half of the world's species of turtles and tortoises are judged to be threatened with extinction (Rhodin *et al.* 2018). Australian freshwater turtles are no exception, with 44% of recognised species formally listed as Vulnerable, Endangered or Critically Endangered by Australian national, state and territory governments or by the International Union for Conservation of Nature (van Dyke *et al.* 2018). Knowledge of the conservation status of Australian freshwater turtles is also incomplete, with some species listed as Data Deficient in one or more jurisdictions.

Globally, freshwater turtles face a plethora of threats, including the loss, degradation and fragmentation of their habitats, overharvesting for food, traditional medicines or the pet trade, climate change, road traffic, predation and disease (Stanford *et al.* 2020). Australian species are vulnerable to all of these threats, but predation by introduced red foxes (*Vulpes vulpes*) has drawn particular attention since Thompson's (1983) estimate that foxes destroyed 93% of nests of eastern long-necked turtles (*Chelodina longicollis*) and Macquarie turtles (*Emydura macquarii*). This figure was based on data from just three locations in South Australia obtained during one or two nesting seasons, but has been extrapolated to assert that 'nest predation rates are extremely high in south-eastern Australia, with >90% of nests destroyed each year' (Spencer 2018) and that 'invasive foxes destroy 95% or more of all turtle nests present in the Murray catchment' (Petrov *et al.* 2018). It has also been used to parameterise population models projecting that foxes will drive some Australian freshwater turtle species to extinction (Spencer *et al.* 2016, 2017).

Vulpes vulpes was introduced to Australia in 1871 and has had a devastating predatory impact on many species of Australian wildlife (Dickman 1996; Saunders *et al.* 2010). Fox predation on eggs of Australian freshwater turtles was reported more than a century ago (Adelaide Advertiser, 3 January 1910, p. 8), and foxes also kill turtles emerging on land to nest or migrate between water bodies (Spencer 2002; Dawson *et al.* 2016). Fox control, principally by poison baiting, is widely practised across Australia but its effectiveness in reducing destruction of freshwater turtle nests is questionable (Robley *et al.* 2016). It is important that assertions that foxes are driving Australian freshwater turtle species to extinction are critically evaluated, because over-statement of the risk posed by foxes could result in resources for turtle conservation being devoted to efforts to reduce fox numbers when they would be more effectively directed elsewhere.

This paper reviews and analyses available information in order to critically evaluate hypotheses that foxes routinely destroy ~95% of nests of Australian freshwater turtles, are more efficient predators of freshwater turtle nests than Australian native predators, and are driving Australian freshwater turtles toward extinction. It then discusses options for increasing recruitment of Australian freshwater turtles where necessary.

Materials and methods

Books, journal papers, reports and theses were consulted for evidence of population trends of Australian freshwater turtles and their causes. Rates of predation on nests of Australian freshwater turtle species, either provided by authors or able to be calculated from data presented, were compiled. For comparative purposes, predation rates were also tabulated for freshwater turtle nests in North America, where foxes and nearly all other nest predators are indigenous. Relevant information was located by combing through the author's collection of documents on Australian and other freshwater turtles, a Google Scholar search using the words 'turtle', 'nest' and 'predation', and screening the reference lists of documents selected by those processes. For North America, the estuarine diamondback terrapin (*Malaclemys terrapin*) and semi-aquatic species such as wood turtles (*Glyptemys insculpta*) were included along with strictly freshwater species. North American studies occasionally reported nest predation rates as proportions of eggs rather than nests, but the two statistics were considered broadly comparable.

Analysis of variance (ANOVA) and the non-parametric Mann–Whitney test were used to compare rates of predation on nests of Australian freshwater turtles between instances where the identified predators included foxes and instances where they did not. Data were not sufficient to include factors such as geographic region or turtle species. ANOVA and the Mann–Whitney test were also used to compare nest predation rates between Australia and North America. The deviation of ANOVA residuals from a normal distribution was assessed with the Shapiro–Wilk test.

Experimental studies monitoring artificial nests constructed by investigators were excluded from these analyses because studies of bird nests cast doubt on the equivalence of predation rates on artificial and natural nests (Berry and Lill 2003). In addition, predation rates on artificial nests can vary considerably depending on nest contents and construction (Spencer 2002; Buzuleciu *et al.* 2016; Edmunds *et al.* 2018). The analyses also excluded rates that were likely to be influenced by artificial reduction, inhibition or exclusion of predators, as well as instances in which losses from predation could not be separated from losses due to other factors such as floods or trampling by cattle. In order to ensure independence of observations, rates for the same turtle species and study area (e.g. for different years or sites) were averaged. Statistical analyses were performed with XLSTAT (Addinsoft 2021).

Results

Reported introduced predators of Australian freshwater turtle nests include cats (*Felis catus*), dogs (*Canis familiaris*) and pigs (*Sus scrofa*), as well as red foxes (*V. vulpes*) (Table 1; see also Parmenter 1985). Native nest predators include Australian magpies (*Gymnorhina tibicen*), crows and ravens (*Corvus* spp.), lapwings (*Vanellus* sp.), monitor lizards (*Varanus* spp.), rakali (*Hydromys chrysogaster*) and southern brown bandicoots (*Isoodon obesulus*) (Table 1; see also Burbidge 1981; Micheli-Campbell *et al.* 2013). Harrington (1933) reported that rats raided nests of *C. longicollis*, but did not specify the rat species or whether it was introduced or native.

Nest predation rates for Australian freshwater turtles (Table 1; $n = 10$) ranged from 20 to 97% and averaged 70 ± 7% overall (mean ± s.e.) or 76 ± 5% for south-eastern Australia only (New South Wales, South Australia and Victoria). Rates were higher where the identified predators included foxes (78 ± 5%) than where they did not (59 ± 15%), but the difference was not statistically significant (ANOVA: $F_{1,8} = 1.91$; $P = 0.21$; Mann–Whitney test: $P = 0.26$). ANOVA residuals deviated only slightly from a normal distribution (Shapiro–Wilk test: $W = 0.97$).

Nest predation rates for North American freshwater turtles (Table 2; $n = 43$) ranged from 17 to 100% and averaged 72 ± 3%. Nest predation rates in Australia and North America did not differ significantly (ANOVA: $F_{1,51} = 0.09$; $P = 0.77$; Mann–Whitney test: $P = 0.71$). ANOVA residuals deviated somewhat

Table 1. Rates of predation on natural nests of Australian freshwater turtle species in the absence of predator control measures.

Turtle species	State or territory	Predation rate (%)	Predators responsible	References
Carettochelys insculpta	Northern Territory	20	*Canis familiaris*, *Varanus* spp.	Doody *et al.* (2004, 2006)
Carettochelys insculpta	Northern Territory	92	*Varanus* spp.	Georges and Kennett (1989)
Chelodina expansa	New South Wales and Victoria	59	Aves, *Hydromys chrysogaster*, *Vulpes vulpes*	Spencer and Thompson (2005)
Chelodina expansa	South Australia	67	*Corvus* sp.	Ercolano (2008)
Chelodina longicollis	New South Wales	83	*Varanus varius*, *Vulpes vulpes*	Vestjens (1977)
Chelodina longicollis	Victoria	84	*Vulpes vulpes*	Chessman (2018)
Chelodina longicollis, *Emydura macquarii*	South Australia	97	*Corvus coronoides*, *Hydromys chrysogaster*, *Varanus* spp., *Vulpes vulpes*	Thompson (1983)
Elseya lavarackorum	Queensland	57	*Sus scrofa*	Freeman (2010)
Emydura macquarii	New South Wales and Victoria	73	*Gymnorhina tibicen*, *Hydromys chrysogaster*, *Vulpes vulpes*	Spencer (2002)
Myuchelys georgesi	New South Wales	69	*Varanus* spp., *Vulpes vulpes*	Blamires *et al.* (2005)

more from a normal distribution for this analysis (Shapiro–Wilk test: $W = 0.93$).

No evidence was found of foxes being the primary driver of population declines of Australian freshwater turtles. For example, decreases in numbers of western swamp turtles (*Pseudemydura umbrina*) in Western Australia since the 1960s have been attributed mainly to habitat loss and contraction of the turtle's annual activity period due to a sharp decrease in winter rainfall, with fox predation noted as a contributing factor (Burbidge 1981; Kuchling 2000; Bouma *et al.* 2020). Excessive collection of eggs for the pet trade in the 1960s and 1970s has been primarily blamed for the low current abundance of the Mary River turtle (*Elusor macrurus*) in Queensland, although anecdotal evidence suggests an increase in nest predation since the 1960s (Flakus 2002). A long-term decline in catch per unit effort (CPUE) of *C. longicollis* in southern New South Wales was attributed primarily to extreme drought in association with anthropogenic flow alteration, whereas the cause of a co-incident decline in CPUE of *E. macquarii* could not be established (Chessman 2011). In eastern New South Wales, a sudden decline of ~90% in the population of Bellinger River snapping turtles (*Myuchelys georgesi*) was caused by an epidemic (Chessman *et al.* 2020).

Moreover, some Australian freshwater turtle populations appear to be stable or increasing, despite exposure to fox predation. For example, no long-term change in CPUE of broad-shelled turtles (*Chelodina expansa*) was observed by Chessman (2011). In the Bellinger River, the population of translocated *E. macquarii* has increased from a few individuals to ~500 in about 30 years (Chessman *et al.* 2020), despite the presence of foxes (Blamires *et al.* 2005). *Emydura macquarii* has also proliferated in other Australian river systems where it has been introduced (Chessman 2021).

Discussion

This review and analysis did not support the hypothesis that foxes routinely destroy ~95% of nests of Australian freshwater turtles. The average nest predation rate across studies was 70%, or 76% for south-eastern Australia only, and these figures include predation by all species, not just foxes. Moreover, nest predation rates may have been overestimated in some studies because depredated nests with excavated soil and scattered eggshells are highly conspicuous (Chessman 2018; Petrov *et al.* 2018), whereas intact nests can be cryptic, particularly if some time has elapsed since nesting (Turner 2004; Spencer 2018). In addition, markers used to facilitate nest monitoring may attract predators (Rollinson and Brooks 2007). Alternatively, however, predation rates may be underestimated if nests are not monitored until the end of the period of hatchling emergence.

Studies of artificial nests were not included in the statistical analysis, but also failed to support a figure of ~95% nest predation by foxes or even by all nest predators combined. For example, Spencer (2002) reported ~55–80% predation on artificial nests containing turtle or quail eggs at Lake Mulwala, New South Wales. Blamires *et al.* (2005) recorded a 73% loss of artificial nests containing chicken eggs on the Bellinger River, New South Wales, from a combination of predation by foxes and monitor lizards, trampling by cattle and flooding. Dawson *et al.* (2014) reported 48–53% predation on artificial nests containing chicken eggs at Chittering Lakes, Western Australia. Robley *et al.* (2016)

Table 2. Rates of predation on natural nests of North American freshwater turtle species in the absence of predator control measures.

Turtle species	Province or state	Predation rate (%)	Predators responsible	References
Chelydra serpentina	Michigan	70	*Procyon lotor*, *Vulpes fulva*	Congdon *et al.* (1987)
Chelydra serpentina	New York	94	*Procyon lotor*	Petokas and Alexander (1980)
Chelydra serpentina	Ontario	84	*Canis latrans*, *Didelphis virginiana*, *Mephitis mephitis*, *Procyon lotor*	Wirsing *et al.* (2012)
Chelydra serpentina	Quebec	84	*Homo sapiens*, *Mephitis mephitis*, *Mustela vison*, *Procyon lotor*	Robinson and Bider (1988)
Chelydra serpentina	South Dakota	69	*Mephitis mephitis*, *Mustela vison*, *Procyon lotor*, *Spilogale putorius*	Hammer (1969)
Chelydra serpentina	Virginia	32	Not reported	Thompson *et al.* (2017)
Chelydra serpentina, *Kinosternon subrubrum*, *Pseudemys floridana*, *Sternotherus odoratus*, *Trachemys scripta*	South Carolina	82	*Procyon lotor*	Tuberville and Burke (1994)
Chrysemys picta	Illinois	78	*Elaphe vulpina*, *Mephitis mephitis*, *Procyon lotor*	Kolbe and Janzen (2002); Bowen and Janzen (2005); Schwanz *et al.* (2010); Strickland and Janzen (2010); Strickland *et al.* (2010); Voves *et al.* (2016)
Chrysemys picta	Illinois	99	Not reported	Refsnider *et al.* (2015)
Chrysemys picta	Michigan	17	*Procyon lotor*	Rowe *et al.* (2005)
Chrysemys picta	Michigan	21	Not reported	Tinkle *et al.* (1981)
Chrysemys picta	Michigan	45	*Mephitis mephitis*, *Procyon lotor*, *Tamias striatus*, *Vulpes fulva*	Snow (1982)
Chrysemys picta	Minnesota	53	*Ictidomys tridecemlineatus*	Refsnider *et al.* (2015)
Chrysemys picta	Ontario	57	*Canis latrans*, *Mephitis mephitis*, *Procyon lotor*	Wirsing *et al.* (2012)
Chrysemys picta	Quebec	44	*Mephitis mephitis*, *Procyon lotor*	Christens and Bider (1987)
Emydoidea blandingii	Michigan	78	Formicidae, *Procyon lotor*, *Urocyon cinereoargenteus*, *Vulpes fulva*	Congdon *et al.* (1983, 2000)
Emydoidea blandingii	Nova Scotia	65	Not reported	Standing *et al.* (2000)
Emydoidea blandingii	Wisconsin	51	Not reported	Byer *et al.* (2018*a*)
Emydoidea blandingii	Wisconsin	59	Not reported	Reid *et al.* (2016)
Emydoidea blandingii	Wisconsin	100	*Mephitis mephitis*	Ross and Anderson (1990)
Glyptemys insculpta	Ontario	88	Mammalia	Brooks *et al.* (1992)
Glyptemys insculpta	Wisconsin	68	*Mephitis mephitis*	Bougie *et al.* (2020)
Glyptemys muhlenbergii	Maryland	83	Insecta, Mammalia	Byer *et al.* (2018*a*, 2018*b*)
Glyptemys muhlenbergii	New Jersey, Pennsylvania	51	*Blarina brevicauda*, *Microtus pennsylvanicus*, *Procyon lotor*, *Vulpes fulva*	Zappalorti *et al.* (2017)
Glyptemys muhlenbergii	North Carolina	53	*Cambarus* sp., *Didelphis virginiana*, Formicidae, Mammalia (small), *Mephitis mephitis*, *Procyon lotor*	Knoerr *et al.* (2021)
Graptemys flavimaculata	Mississippi	62	*Corvus ossifragus*, *Lampropeltis getula*, *Solenopsis invicta*	Horne *et al.* (2003)
Graptemys geographica, *Graptemys ouachitensis*	Wisconsin	90	*Procyon lotor*	Geller (2012*a*)
Graptemys oculifera	Mississippi	98	Canidae, *Corvus brachyrhynchus*, *Corvus ossifragus*, *Dasypus novemcinctus*, *Homo sapiens*, *Lampropeltis getula*, *Procyon lotor*, *Solenopsis molesta*, *Tripanurga importuna*	Jones (2006)
Graptemys ouachitensis	Wisconsin	95	*Procyon lotor*	Geller (2015)
Kinosternon baurii	Florida	100	*Procyon lotor*, Rodentia or Soricidae, Serpentes	Wilson *et al.* (1999)

(*Continued on next page*)

Table 2. (*Continued*).

Turtle species	Province or state	Predation rate (%)	Predators responsible	References
Kinosternon flavescens	Illinois	100	*Canis latrans*, *Heterodon nasicus*, *Mephitis mephitis*	Tuma (2006)
Kinosternon flavescens	Nebraska	79	*Heterodon nasicus*, Rodentia	Iverson (1991)
Kinosternon subrubrum, *Pseudemys concinna*, *Trachemys scripta*	South Carolina	84	*Procyon lotor*, Soricidae?	Burke *et al.* (1998)
Malaclemys terrapin	Florida	85	*Corvus brachyrhynchos*, *Corvus ossifragus*, *Dasypus novemcinctus*, *Ocypode quadrata*, *Procyon lotor*, *Quiscalus major*, *Solenopsis invicta*	Butler *et al.* (2004); Munscher *et al.* (2012)
Malaclemys terrapin	Georgia	62	Not reported	Crawford *et al.* (2014)
Malaclemys terrapin	New Jersey	61	*Corvus brachyrhynchos*, *Larus atricilla*, *Procyon lotor*, *Vulpes fulva*	Burger (1977)
Malaclemys terrapin	New York	84	*Procyon lotor*	Feinberg and Burke (2003); Burke *et al.* (2015); Edmunds *et al.* (2018)
Malaclemys terrapin	Virginia	80	Aves, *Procyon lotor*	Ruzicka 2006
Pseudemys concinna	Florida	100	*Corvus ossifragus*, *Procyon lotor*, *Scalopus aquaticus*, *Solenopsis* sp.	Jackson and Walker (1997)
Pseudemys floridana	Florida	100	*Procyon lotor*, *Solenopsis invicta*	Aresco (2004)
Pseudemys texana, *Trachemys scripta*	Texas	33	*Procyon lotor*	Washington (2008)
Sternotherus odoratus	Pennsylvania	78	Not reported	Ernst (1986)
Trachemys scripta	Florida	97	*Procyon lotor*, *Solenopsis invicta*	Aresco (2004)

recorded 84% loss of artificial nests containing quail eggs at Hattah Lakes, Victoria, in the absence of fox control measures. Data graphed by Spencer *et al.* (2017) suggest an average depredation of ~80% for artificial nests containing chicken or quail eggs in New South Wales and Victoria. As for natural nests, the average over all of these artificial-nest studies is ~70% for all predators combined.

Supporting evidence was also lacking for the proposition that foxes are more efficient nest predators than Australian native birds, marsupials, monitor lizards and rodents. The lack of a statistically significant difference in Australian nest predation rates between instances where foxes were among the identified nest predators and instances where they were not might reflect the very small sample size, the role of other introduced predators, or incomplete detection of predator species, as well as the efficiency of native nest predators. However, it is clear that native species can destroy a large proportion of turtle nests. For example, monitor lizards had raided 11 of 12 nests of the pig-nosed turtle (*Carettochelys insculpta*) in Kakadu National Park, Northern Territory (Georges and Kennett 1989), and 18 of 24 nests of *C. longicollis* at Lake Cowal, New South Wales (Vestjens 1977). Lyndon (1966) and Beck (1991) both reported ravens (*Corvus* spp.) as voracious predators of *C. longicollis* nests. It is also likely that foxes have partly substituted for Australian native nest predators, because foxes have reduced or even eliminated populations of native species that are known or likely to prey on turtle nests, such as bandicoots, monitor lizards and quolls (*Dasyurus* spp.) (Dickman 1996; Saunders *et al.* 2010). Thus, fox suppression can increase populations of these native nest predators (Bowler 2016; Hu *et al.* 2019; Madden Hof *et al.* 2020). Large native marsupial predators (*Sarcophilus harrisii* and *Thylacinus cynocephalus*), which became extinct on mainland Australia soon after the introduction of dogs (dingoes) about 3500 years ago, might also have preyed on turtle nests (Burbidge 1981; Thompson 1983).

Nest predation rates also did not differ significantly between Australia and North America, where freshwater turtle nests are preyed on by a plethora of native arthropod, avian, mammalian and reptilian nest predators, including coyotes (*Canis latrans*), crows (*Corvus* spp.), mink (*Mustela vison*), North American red foxes (*Vulpes fulva*, sometimes assigned to *V. vulpes*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) (Table 2). Some of these predators also take nesting turtles (e.g. Karson *et al.* 2018; Mullin *et al.* 2020).

If average nest predation rates are equivalent in Australia and North America, and North American turtles have been able to persist for millennia in sympatry with foxes and a panoply of other predators, why would foxes be able to drive Australian freshwater turtles to extinction? Spencer *et al.* (2016) maintain that Australian turtles such as *E. macquarii* are especially vulnerable to fox predation because they employ an ‘arribada’ strategy of synchronous and spatially concentrated mass nesting, like that of some sea turtles (Eckrich and Owens 1995). They suggest that this strategy evolved to protect some nests by saturating native nest predators, but fails to do so in the case of foxes, thereby constituting an ‘ethological trap’ that will eventually drive *E. macquarii* to extinction. However, an empirical study in Québec, Canada, concluded that synchronous nesting *increased* survival of nests of snapping turtles (*Chelydra serpentina*) that were preyed on by a suite of efficient predators including *M. mephitis*, *M. vison* and *P. lotor* (Robinson and Bider 1988). Moreover, nesting of *E. macquarii* is spread over about 2 months in the south of its distribution and 4 months further north, with females producing up to three clutches of eggs annually (Chessman 1978; Georges 1983; Booth 2010). Its nesting is triggered by rainfall (McCosker 2002; Bowen *et al.* 2005; Booth 2010), as in many other freshwater turtle species (Czaja *et al.* 2018), and is therefore concentrated during rain events. However, there is no evidence that *E. macquarii* migrates to nest communally in the manner of some sea turtles. Nesting during rain is probably adaptive regardless of the species of nest predator, because heavy rain softens soil to facilitate nest excavation, and can disguise nests from predators (Legler 1954; Bowen and Janzen 2005; Czaja *et al.* 2018).

Although the impact of foxes on nests of Australian freshwater turtles appears to have been exaggerated, it is clear that foxes have a substantial impact on turtle recruitment and survival, except in the far north of the continent where foxes are absent and feral pigs are the chief introduced predator (Fordham *et al.* 2006). In addition, some fox populations may be enhanced by mesopredator release due to suppression of Australia’s apex terrestrial predators, dingoes and other wild dogs (Wallach *et al.* 2010; Letnic *et al.* 2011; though see Allen *et al.* 2013). Furthermore, foxes may benefit from anthropogenic food subsidies (Oro *et al.* 2013), which they widely exploit (Fleming *et al.* 2021). Consequently, the pressure of fox predation on turtle nests is likely to be spatially variable and intense in some regions.

How should nest predation be curtailed where research shows that increased recruitment is necessary for the persistence or recovery of Australian freshwater turtle populations? Many methods are used to control foxes across Australia for both wildlife conservation and livestock protection, including exclusion fencing, den fumigation, shooting, trapping and stationing of guard animals. However, the deployment of meat baits poisoned with sodium fluoroacetate (1080) is most popular because of its cost effectiveness (Saunders *et al.* 2010). Controlling fox numbers with poison baits has been found to lower predation on nests of both freshwater and marine turtles in Australia (Spencer 2002; Madden Hof *et al.* 2020), but a major fox-baiting programme at the Hattah Lakes in Victoria did not significantly reduce predation on artificial turtle nests (Robley *et al.* 2016). Spencer *et al.* (2017) suggested that poison baiting may be ineffective unless it results in the near elimination of the fox population because predation on artificial nests was independent of fox abundance unless the latter was extremely low. In addition, baits are often consumed by non-target species (Dundas *et al.* 2014; Millar *et al.* 2015), and foxes can rapidly immigrate to re-populate areas where baiting has been undertaken (Gentle *et al.* 2007), or develop bait avoidance or toxin tolerance (Allsop *et al.* 2017). Thus, effective reduction of turtle nest predation by fox baiting suffers from many practical constraints.

Excluding foxes from nesting areas through fencing can be effective (Palmer-Allen *et al.* 1991), but can also produce perverse outcomes. For example, a predator-exclusion fence surrounding a reserve in the Australian Capital Territory intercepted and killed migrating *C. longicollis*, apparently by making them overheat (Ferronato *et al.* 2014). In Western Australia, the installation of fox-exclusion fences around reserves to protect *P. umbrina* led to population increases of other predators inside the reserves: native bandicoots (*I. obesulus*) and ravens (*Corvus coronoides*), and introduced rats (*Rattus* spp.) (Kuchling 2000; Bowler 2016). Electric fencing of nesting areas (Geller 2012*b*) can provide a targeted way to reduce nest predation, and such fences can be removed if necessary once hatchlings have emerged.

Locating intact turtle nests and covering them with predator-exclusion screens or cages can also be effective for inhibiting both foxes and other predators (Graham 1997; Riley and Litzgus 2013). This technique proved more effective than lethal fox control via trapping and den fumigation for protecting eggs of Australian sea turtles (O’Connor *et al.* 2017). However, predation on hatchlings after their emergence from protected nests may limit the benefits in some circumstances (Campbell *et al.* 2020), and care may be needed to avoid attracting illegal egg or hatchling collectors (Flakus 2002).

Another option for increasing turtle recruitment is to bypass reproduction-related predation entirely by capturing gravid females in the wild and inducing their oviposition with hormone injections (Ewert and Legler 1978). The eggs so obtained can be artificially incubated, and the resulting hatchlings can be released in habitats where they have the best chance of survival, or else head-started; i.e. kept in captivity until they grow big enough to resist most predators (Buhlmann *et al.* 2015; Carstairs *et al.* 2019). In extreme cases, captive breeding may be necessary (Kuchling 2000; Chessman *et al.* 2020).

Research is needed to better understand the biological and environmental factors that regulate recruitment and survival of Australian freshwater turtles, and why some turtle populations are able to increase despite exposure to fox predation, while others seem unable to do so. Spencer *et al.* (2016) suggested that *C. expansa* is less vulnerable than *E. macquarii* to nest predation by foxes because nests of *C. expansa* are more widely scattered. However, available evidence shows population stability for *C. expansa* (Chessman 2011) and increases for *E. macquarii* in some instances (Chessman *et al.* 2020; Chessman 2021). It is important that assessments of nest predation rates extend for several years, because inter-annual variation in rates can be enormous (e.g. Congdon *et al.* 2000; Schwanz *et al.* 2010).

Conclusions and recommendations

Assertions that red foxes consistently cause ~95% depredation of the nests of freshwater turtles in south-eastern Australia and are thereby driving turtle species to extinction, are not supported by the available evidence. Documented declines of Australian freshwater turtle populations have mainly been attributed to factors other than fox predation, and population models forecasting fox-induced extinction are based on what appear to be inflated nest predation rates. Where research shows that increased recruitment is necessary for the persistence or recovery of populations of Australian freshwater turtles, strategies such as electric fencing of nesting beaches, caging of nests, artificial incubation of eggs, and head-starting of juvenile turtles will probably be more cost-effective than efforts to reduce fox numbers.

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Data availability. The data analysed are available in the cited works.

Conflicts of interest. The author declares no conflicts of interest.

Declaration of funding. This research did not receive any specific funding.

Acknowledgements. The anonymous reviewers are thanked for their helpful comments on the initial submission of this paper.

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