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

Damien A. Fordham[1,2], Arthur Georges[1,*] and Barry W.Brook[2,3]

[1]*Institute for Applied Ecology, University of Canberra, ACT 2601, Australia;* [2]*School for Environmental Research, Institute of Advanced Studies, Charles Darwin University, Darwin NT 0909, Australia; and* [3]*Research Institute for Climate Change and Sustainability, School of Earth & Environmental Sciences, University of Adelaide, South Australia 5005, Australia*

Summary

1. Until recently, the northern snake-necked turtle (*Chelodina rugosa* Ogilby, 1890) provided a seasonal source of protein for indigenous communities in tropical northern Australia. Today, feral pigs (*Sus scrofa* Linnaeus, 1758) exert a heavy predation pressure on *C. rugosa*, compromising subsistence harvest rates and threatening local persistence.

2. We investigated the influence of pig predation and harvest (subsistence and commercial) on *C. rugosa* persistence at discrete water holes using a stage-based matrix population model. Vital rates varied with wet season rainfall, pig predation and harvest. In addition, hatchling survival was density-dependent.

3. We show that field-based estimates of pig-related turtle mortality exceed levels that can be offset by increased hatchling survival, leading to predictions of rapid population decline and certain elimination of affected populations within 50 years.

4. Conversely, in the absence of pigs, compensatory increases in hatchling survival were sufficient to allow an annual harvest of up to 20% of subadult and adult *C. rugosa* without causing extirpation or substantial population suppression.

5. *Synthesis and applications.* This demographic modelling shows that periodic local culling of pigs, fencing of wetlands to exclude predators, and hatchling supplementation to offset losses from predation are all viable management strategies for ensuring ongoing turtle harvests. Such demonstrations of the potential resilience of long-lived vertebrates under a properly managed harvest regime is important to convince natural resource agencies that conservation management for long-term viability need not exclude some degree of consumptive use. These findings are broadly relevant to applied ecology, providing important implications for the management of wildlife species subject to competing ecological pressures, such as subsistence and commercial harvesting and predation by invasive species.

Key-words: Chelidae, density dependence, exploitation, matrix model, population viability analysis (PVA), recruitment, regulation, subsistence; wildlife utilization

Introduction

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

*Correspondence author. E-mail: georges@aerg.canberra.edu.au

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

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

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

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

Methods

ECOLOGICAL SYSTEM

Chelodina rugosa attains high densities in the ephemeral swamps and other wetlands of tropical northern Australia (Cogger 2000) and the Fly Delta of New Guinea (Georges *et al.* 2006) (Fig. S1 in Supplementary Material). Turtle activity is punctuated each year by the dry season, when the wetlands recede and often dry out completely. Immediately before drying, turtles move to the shallows, bury themselves in the mud and aestivate (Kennett & Christian 1994). At sites where pig abundance is high, pigs prey heavily on turtles, reducing survival during the weeks before drying (Fordham *et al.* 2006b). At sites of low pig abundance, subsistence harvesting reduces the survival of aestivating turtles (Fordham *et al.* 2007a). Reproduction coincides with the wet season, when wetlands refill and food availability is high (Fordham, Georges & Corey 2006a). The timing and quality of rainfall in the wet–dry tropics is highly variable both within and across years (Taylor & Tulloch 1985; Fig. 1). In unusually wet years, wetlands do not dry, turtles do not aestivate, harvesting and pig predation are limited, and thus turtle survival remains high (Fordham *et al.* 2007a).

MODEL STRUCTURE

We used stage- and sex-structured matrix models to explore the impact of harvesting and pig predation on *C. rugosa*. Stage-structured matrices are commonly used to model turtle population growth, because chelonians are often difficult to age and display distinct life-history traits such as sexual dimorphism and size-dependent maturity and survival (e.g. Cunnington & Brooks 1996). The transition probabilities of stage-based models incorporate the probability of making a transition from one stage to the next between times i and $i + 1$, conditional on surviving (Nichols *et al.* 1992). The probability of surviving and remaining in the same stage (P) and the probability of surviving and moving into the next stage (G) were calculated for stages 1–6 using the equations:

$$P_i = \left(\frac{1 - \Phi_i^{d_i - 1}}{1 - \Phi_i^{d_i}} \right) \Phi_i \qquad \text{eqn 1}$$
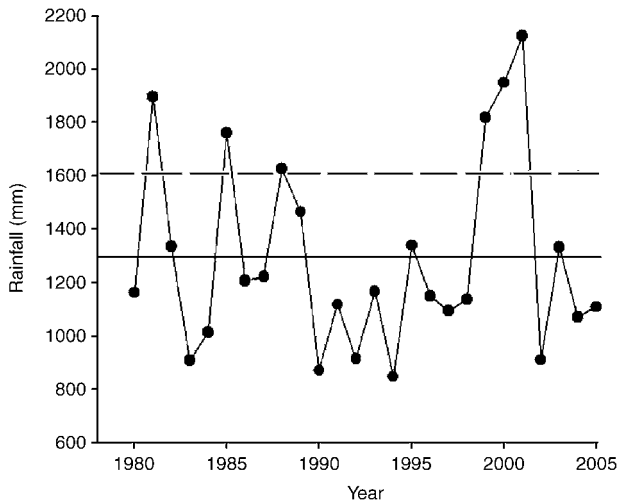
Fig. 1. Annual rainfall in the Maningrida region 1980–2005 (Australian Bureau of Meteorology, unpublished data). Horizontal line, mean annual rainfall (1290 mm); dashed line, 125% of mean annual rainfall.

$$G_i = \frac{\Phi_i^{d_i}(1 - \Phi_i)}{1 - \Phi_i^{d_i}} \qquad \text{eqn 2}$$

where Φ is survival and d_i is the number of years from stage i to $i + 1$ (Crouse *et al.* 1987).

The matrix model consisted of four female stages. Stage 1 (S_1) represented pooled yearlings and 2-year-old juvenile females (carapace length, CL < 140 mm); S_2) subadult females (CL = 140–180 mm); S_3, small adult females (CL = 180–220 mm); S_4, large adult females (CL = 220 mm). The model had two male stages: S_5 corresponded to pooled yearlings and 2-year-old juvenile males (CL < 140 mm); S_6 represented mature males (CL = 140 mm). Female reproductive stages each had a fecundity rate ($F = 0.5F_{male}$ and $0.5F_{female}$). Egg mortality and hatchling survival (0-year-olds) were included in the

fecundity parameter. The transition matrix A, describing the flux of individuals from one year to the next, took the form:

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

DEMOGRAPHIC PARAMETERS

We assumed that emigration and immigration were minimal because of (1) the choice of study sites (discrete, isolated billabongs; Fordham *et al.* 2007a); and (2) the fact that *C. rugosa* tend to aestivate rather than disperse in response to the periodic absence of water (Fordham *et al.* 2006b). The impact of drying, pig predation and harvest on the survival of stages S_1–S_6 were based on detailed capture–mark–recapture studies (Fordham *et al.* 2006b, 2007a; Table 1). Growth in *C. rugosa* is sexually dimorphic: males approach asymptotic size earlier and at a smaller size than females (Kennett 1996). Estimates of male and female growth rates from the Giddadella site (Fordham *et al.* 2007a) were used in the model. Size of female maturity in *C. rugosa* is an evolved response that promotes demographic resilience under conditions of comparatively low survival (Fordham 2007; Fordham *et al.* 2007a). Small females (CL = 180–200 mm) were treated as mature in the model. Fecundity rate was derived as the product of mean clutch size (*m*), sex ratio (*sr*), proportion of reproductively active females (*r*) and hatchling survival (Φ_0). Clutch size is strongly correlated with body size (Fordham *et al.* 2007a). Mean clutch size for S_3 and S_4 was 10·18 and 14·01, respectively (number of clutches = 62 and 84). The proportion of reproductively active females of mature size was set at 0·7, based on field observations ranging from 0·53 to 0·88 (Fordham 2007). We assumed a 50 : 50 sex ratio at birth. Offspring sex of all chelid turtles examined so far is determined genetically (Georges 1988; Georges & McInnes 1998).

Table 1. Cormack–Jolly–Seber and live–recapture and dead recovery survival estimates for *Chelodina rugosa* under different subsistence harvest and predation scenarios (after Fordham *et al.* 2006b; Fordham *et al.* 2007a)

Scenario	Percentage	Survival	Stage	Estimate	SE
Wet		Juvenile	$S_{1,5}$	0·930	0·0281
		Adult	$S_{2–4,6}$	0·930	0·0281
Dry		Juvenile	$S_{1,5}$	0·834	0·037
		Adult	$S_{2–4,6}$	0·834	0·037
Dry harvested	20	Juvenile	$S_{1,5}$	0·834	0·037
		Adult	$S_{2–4,6}$	0·634	0·037
Dry harvested	30	Juvenile	$S_{1,5}$	0·834	0·037
		Adult	$S_{2–4,6}$	0·534	0·037
Dry harvested	40	Juvenile	$S_{1,5}$	0·834	0·037
		Adult	$S_{2–4,6}$	0·434	0·037
Dry pig predation	48	Juvenile	$S_{1,5}$	0·501	0·082
		Adult	$S_{2–4,6}$	0·501	0·082
Dry pig predation	58	Juvenile	$S_{1,5}$	0·396	0·099
		Adult	$S_{2–4,6}$	0·396	0·099
Dry pig predation	73	Juvenile	$S_{1,5}$	0·24	0·069
		Adult	$S_{2–4,6}$	0·24	0·069

S_1 and S_5 represent yearlings and 2-year-old juvenile females and males (carapace length, CL < 140 mm); S_2, subadult females (CL = 140–180 mm); S_3, small adult females (CL = 180–220 mm); S_4, large adult females (CL = 220 mm); S_6, mature males (CL = 140 mm). Mortality due to subsistence harvest by people is additive, whereas pig predation is partly compensatory.

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

$$H = [(N_3 \times m_3 \times r) + (N_4 \times m_4 \times r)] \times h \qquad \text{(eqn 3)}$$

DENSITY DEPENDENCE

Hatchling survival in *C. rugosa* is strongly density-dependent, while adult survival and fecundity are density-independent (Fordham 2007). Cormack–Jolly–Seber capture–mark–recapture analysis prior to and after population manipulation at Imimbar and Ginmilly billabongs, and live recapture and dead recovery (Burnham Models; Burnham 1993) analysis prior to and after a rare harvest event at Murrybulljuluk, allowed hatchling survival (Φ_0) to be estimated when population size (N) was at 32% ($\Phi_0 = 0.30$), 43% ($\Phi_0 = 0.10$), 78% ($\Phi_0 = 0.14$) and 100% ($\Phi_0 = 0.01$) of estimated carrying capacity (Fordham 2007; Fordham *et al.* 2007a). Hatchling survival at very low densities (1%) was assumed to be high ($\Phi_0 = 0.93$; Table 1). The relationship between density and log survival was strongly linear ($r^2 = 0.936$) and thus a linear density dependent decay function was used to model the relationship between Φ_0 and N:

$$\Phi_0 = a \times \exp(b \times N) \qquad \text{(eqn 4)}$$

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

ENVIRONMENTAL STOCHASTICITY

The wet–dry tropics of northern Australia experience extremes of high rainfall during the monsoonal wet seasons and the near absence of rainfall in the intervening dry seasons. The timing of the onset, duration and severity of the wet season dictates the presence or absence of water at wetlands at the end of the following dry season, in turn influencing *C. rugosa* survival (Fordham *et al.* 2006b). Local rainfall records for Maningrida (1980–2005; Australian Bureau of Meteorology, unpublished data; Fig. 1) were used to estimate drying frequency. If wet season rainfall exceeded 125% of the average (1290 mm), the year was classed as a 'wet year' and it was assumed that billabongs (waterholes) did not dry. This method resulted in six 'wet years' between 1980 and 2005, at a frequency of 0.23.

PIG PREDATION

In areas of high pig abundance, pig predation accounts for 96% of *C. rugosa* fatalities in dry years (CL > 100 mm; Fordham *et al.* 2006b). However, pig predation occurs at a time when this mortality is partially compensatory to other forms of predation and harvest

(Fordham *et al.* 2006b; Fordham *et al.* 2007a). Pig predation at Giddadella, in years of high pig abundance, occurred at an estimated rate of 48% of S_{1-6} (CI = 23–72%; Fordham *et al.* 2007a) providing an additional 33% (CI = 7–58%) mortality above background rates. In some years, pig predation may be as high as 73% (CI = 59–85%; Fordham *et al.* 2006b), causing an additional 56% (CI = 43–70%) mortality. At Damdam, pig predation was estimated to be 58% (CI = 36–78%; Fordham *et al.* 2007a) causing an additional 44% (CI = 21–63%) mortality.

HARVEST

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

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

MODEL SCENARIOS

Separate matrices were constructed for (1) wet years; (2) dry years; (3) dry years with low pig abundance and no harvesting; (4) dry years with high pig abundance; (5) dry years with subsistence harvesting; (6) wet years with commercial harvesting; and (7) dry years with commercial harvesting. Wet years were modelled at a frequency of 0.23 (see Environmental stochasticity). The model was developed and simulated in R (R Development Core Team 2005). Life-stage simulation analysis was used to account for uncertainty in the estimates of age and survival (Wisdom, Mills & Doak 2000). The ages of S_1 turtles were varied by sampling parameters from a uniform distribution with ranges of 1–1.4 years; 1.6–2.2 years for S_2; 3.5–5.1 years for S_3; and 1.6–1.9 years for S_5 (based on Fordham *et al.* 2007a). Survival estimates for wet years were likewise varied between $\Phi_{1-6} = 0.783$–0.977; $\Phi_{1-6} = 0.746$–0.895 for dry years with no harvest or pig predation; $\Phi_{1-6} = 0.134$–0.784 for dry years with pig predation; $\Phi_{2,3,4,6} = 0.334$–0.834; and $\Phi_{1,5} = 0.746$–0.895 for dry years with harvests (subsistence and commercial) of 0–50% turtles (CL ≥ 140 mm) (based on Fordham *et al.* 2006b, 2007a). Stochastic simulations were projected over a period of 50 years, and the number of iterations was set at 10 000 unless otherwise stated. Initial population size was set at 99, with a stable stage structure, and carrying capacity at 288 individuals, based on abundance estimates

at Giddadella (Fordham 2007). The R model script is available from the authors on request.

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

1. no pig predation or subsistence hunting

2. pig predation at a rate of 20–85% of the total population size of turtles with CL > 100 mm

3. subsistence harvests at a rate of 0–50% of turtles (CL ≥ 140 mm) each dry year and in 50% of dry years

4. commercial harvests at a rate of 0–50% of turtles (CL ≥ 140 mm) each year and every second year.

The past impact of field estimates of subsistence turtle harvesting and pig predation (Fordham *et al.* 2007a) on population persistence was simulated retrospectively using the 26-year sequence of wet–dry rainfall categories in the Maningrida region, providing insight into the impact of extensive dry periods coupled with consecutive wet years (Fig. 1). As an alternative harvest strategy, we also modelled the number of subadult and adult turtles (evenly pooled across S_2, S_4 and S_6) that can be taken annually as a constant offtake without threat to persistence. In this case, harvest occurred only when the population size exceeded 100 individuals.

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

We report the extirpation probability (EP) and expected minimum population size (EMS) and percentage decrease in EMS value as the main measures of risk to population decline for each scenario. We calculated EMS by taking the smallest population size observed for each iteration and averaging these minima (McCarthy & Thompson 2001); the output is equivalent to the area under the quasi-extinction curve (McCarthy 1996). Population decline was measured as percentage decrease in EMS value from the initial population size (McCarthy & Thompson 2001). We also report the average median population size for each scenario.

Results

PIG PREDATION

Pig predation at levels ≥40% is predicted to cause extirpation or substantial population suppression of *C. rugosa* within 50 years (Fig. 2; Table 2). The regularity of flooding would have to increase fourfold to provide a sufficient number of refugial years to prevent population decline and possibly extirpation as a result of pig predation rates ≥50% in dry years (Fig. 2).
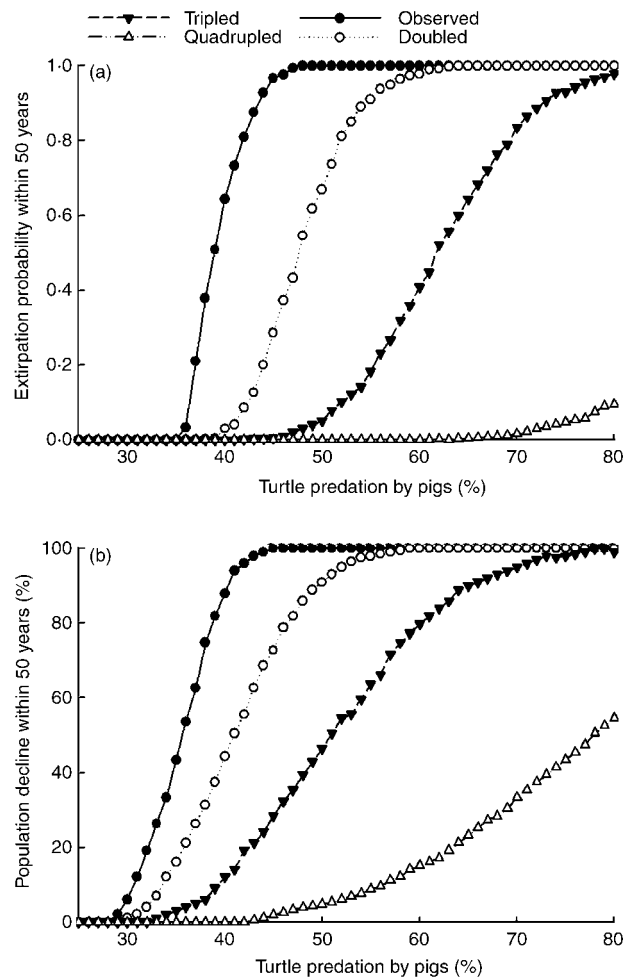

Fig. 2. Probability of extirpation (a) and predicted population decline (b) under different pig predation rates and regularity of flooding. Pig predation was simulated separately (60 000 simulations) as a proportion of the turtle population (turtles with CL ≥ 100 mm) ranging from 20 to 85% of turtles (lower and upper bounds of estimates of pig predation; see Methods) under four flooding scenarios: wet years occurring at a frequency of 0·23 (observed), 0·46 (doubled), 0·69 (tripled) and 0·92 (quadrupled). Note that predation rates ≥40%, under the present flooding regime, are projected to cause extirpation or substantial population decline; and that flooding events would have to increase fourfold to provide a sufficient number of refugial years to prevent substantial population decline, and possibly extirpation, if pig predation rates are ≥50% in dry years.

HARVEST

A 20% subsistence harvest of adult and subadult turtles (CL = 140 mm) each dry year represented no threat to population persistence (EP = 0; EMS = 84; 15% population decline; Table 2). Harvesting at this rate in 50% of dry years had little impact on population size (EP = 0; EMS = 97; 2% decline). A harvest rate of 30% each dry year caused population size to decline substantially, leading to possible extirpation (EP = 0·298; EMS = 24; 76% decline), but harvesting in only half of all dry years at this rate mitigated this impact (EP = 0; EMS = 75; 24% decline). A harvest rate of 40% each

Table 2. Scenarios for future exploitation and predation of *Chelodina rugosa* based on population modelling

Scenario	Percentage	EP	EMS	Population decrease (%)	Median population size
No harvest and no pig predation		0·000	**	**	185 (136–235)
Pig predation	20	0·000	**	**	159 (140–200)
	30	0·000	91	8	107 (85–157)
	40	0·596	11	89	34 (14–99)
	50	1·000	0	100	11 (7–33)
Customary harvest every dry year	20	0·000	84	15	100 (73–147)
	30	0·298	24	76	50 (16–107)
	40	0·982	0	100	16 (9–53)
Customary harvest in 50% of dry years	20	0·000	97	2	144 (100–203)
	30	0·000	75	24	118 (65–189)
	40	0·108	42	58	87 (20–174)
Annual commercial harvest	20	0·000	82	17	90 (69–109)
	30	0·395	18	82	32 (14–61)
	40	0·996	0	100	11 (8–16)
Commercial harvest every second year	20	0·000	95	4	129 (92–180)
	30	0·017	62	37	96 (45–160)
	40	0·353	25	75	60 (14–138)

**Population size increased.
Extirpation probability (EP), expected minimum population size (EMS) and population decline (percentage decrease in EMS value from initial population size), and projected median population size (10 000 model simulations) are described for each scenario. Numbers in parentheses are 95% simulation quantiles. Note that populations can be subsistence harvested in dry years at a rate of 20%. If harvesting occurs in 50% of dry years, populations can be taken at a rate of 30% without causing substantial population suppression. Pig predation rates ≥40% will cause extirpation or substantial population suppression if management institutions are not implemented. It is sustainable to harvest turtle populations commercially at an annual rate of 20%, provided pig predation and subsistence harvest are absent.

dry year caused extirpation (EP = 0·982; EMS = 0) and severe population reduction (EP = 0·108; EMS = 42; 58% decline) when it occurred in only 50% of dry years. Therefore subsistence harvesting at rates >20% in all dry years poses a threat to persistence (Fig. 3). If harvesting is conducted in 50% of dry years, populations can be harvested at a rate of 30% without threat of extirpation (Fig. 3). The retrospective projection, based on the sequence of flooding events observed in the Maningrida region over the past 26 years, confirmed that subsistence harvesting at a rate of 20% is sustainable even when nine consecutive dry (harvested) years occurred (Fig. 4).

If pig predation and subsistence harvests are non-existent, the model predicts that *C. rugosa* (CL = 140 mm) can be harvested commercially at an annual rate of 20% without any threat of extirpation (EP = 0; EMS = 82; 17% decline; Table 2; Fig. 3), or at 30% if harvesting occurs every second year (EP = 0·017; EMS = 62; 37% decline). Commercial harvesting at a rate of 40%, even if conducted only every second year, resulted in severe population decline, threatening extirpation (EP = 0·353; EMS = 25; 75% decline; Table 2). An annual commercial harvest of up to 30 turtles (constant offtake) did not substantially affect population size (EMS = 69; decline = 30%) provided harvest ceased at low numbers. Harvest rates of ≥40 turtles consistently caused substantial decline (EMS = 54; decline = 40%). If constant numbers of individuals were always removed (irrespective of current population size), extirpation was almost inevitable (EP = 0·838) when the constant offtake rate was ≥8 individuals per year.

HEADSTARTING HATCHLINGS

The annual release of 58 yearlings would be enough to prevent extirpation in turtle populations that incur a pig predation rate of 50% (EP = 0; EMS = 97; 2% decline; Table 3). Annually releasing 71 yearlings would offset a pig predation rate of 60% (EP = 0; EMS = 95; 4% decline), while 84 yearlings would be need to offset a 70% predation rate (EP = 0; EMS = 94; 5% decline). Turtle populations could be harvested commercially at annual rates of 30 and 40% if 23 and 32 yearlings, respectively, were released into the population each year (Table 3). Therefore headstarting programmes provide an effective conservation strategy for *C. rugosa* populations in regions of high pig abundance, and could be used to increase commercial or traditional harvest yields of adults.

Discussion

Freshwater turtle harvesting has been widely criticised because of unfavourable life-history traits (Cunnington & Brooks 1996; Heppell 1998) and a presumed negligible compensatory response to harvest (Congdon *et al.* 1993, 1994). We demonstrate clearly that compensatory increases in hatchling survival are sufficient to allow annual stage-specific harvests of up to 20% of subadult and adult *C. rugosa*, without causing extirpation or substantial population suppression. We provide predictive evidence that subsistence harvest rates are sustainable, strengthening our assertion that density-dependent compensatory strategies at least partly underlie the persistence of *C. rugosa* throughout a long period
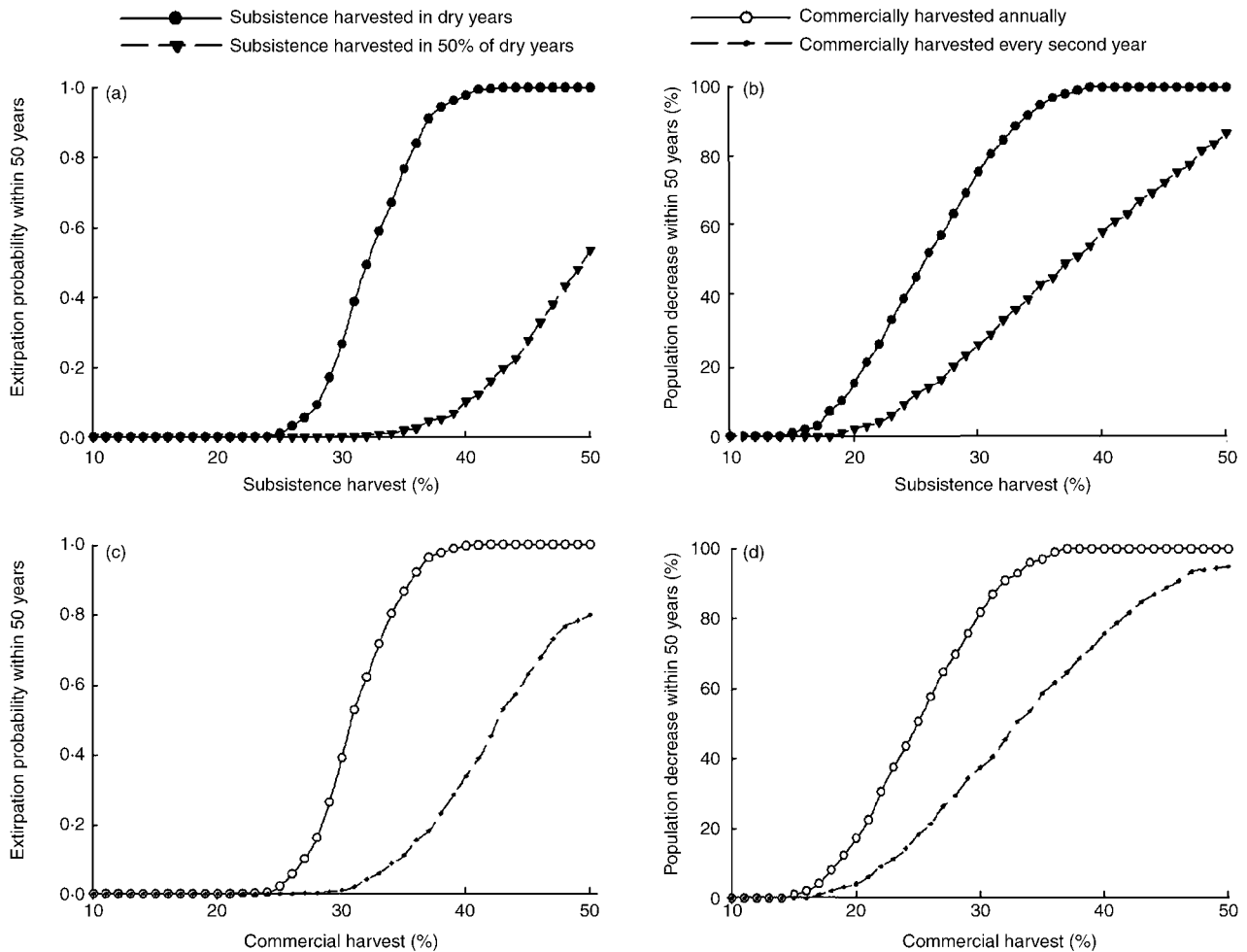
Fig. 3. Probability of extirpation (a,c) and predicted population decline (b,d) owing to subsistence (a,b) and commercial harvests (c,d). Harvest rates were simulated (60 000 simulations) as a proportion (0–50%) of the turtle population (CL ≥ 140 mm). Subsistence harvests were modelled in all dry years and every second dry year. Commercial harvests were modelled annually and biannually. Note that subsistence harvesting 20% of subadult and adult turtles in dry years, or commercial harvesting 20% annually, does not result in substantial population decline.

Table 3. Number of additional yearlings needed to offset pig predation and annual commercial harvesting when population size is set at half carrying capacity

Scenario	Percentage	Additional yearlings	EP	EMS	Population decrease (%)	Median population size	Final population size
Pig predation	40	42	0	98	1	119 (126–148)	125
	50	58	0	97	2	110 (94–142)	116
	60	71	0	95	4	103 (88–140)	108
	70	84	0	94	5	101 (74–139)	104
Annual commercial harvest	20	13	0	**	**	111 (102–133)	114
	30	23	0	98	1	101 (94–114)	102
	40	32	0	97	2	100 (93–108)	100

**Population size increased.
Extirpation probability (EP), expected minimum population size (EMS) and population decline (percentage decrease in EMS value from initial population size), and projected median population size (10 000 simulations) are described for each scenario. Numbers in parentheses are 95% simulation quantiles.

of interaction with people in tropical northern Australia (Fordham *et al.* 2007a). In contrast, we also show that estimates of turtle predation by pigs (Fordham *et al.* 2006b, 2007a), if left unmanaged, are so high that the extirpation of many *C. rugosa* populations in the near future is all but assured. Management strategies to reduce or offset turtle predation by pigs are therefore an urgent conservation priority.
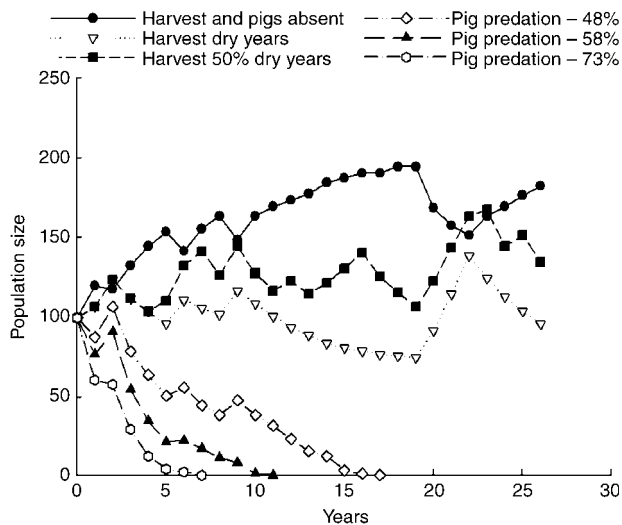
Fig. 4. Population size estimated retrospectively from a starting size of 99, based on a 26-year sequence of wet and dry years in Maningrida, northern Australia. Harvest rate was set to 20% (CL ≥ 140 mm) in dry years. Predation and harvest rates are based on local estimates (Fordham *et al.* 2007a). Note that harvesting dry years was sustainable even when nine consecutive dry years occurred (years 11–19).

Aboriginal harvest rates are regulated by stochastic rainfall, the frequency and timing of ceremonies, and other cultural activities that interfere with harvests (Fordham *et al.* 2006b). Recently, we suggested that these refugial years might be important for maintaining harvested *C. rugosa* populations over the long period of interaction with people in tropical northern Australia (Fordham *et al.* 2006b, 2007a). The model projections presented here demonstrate that a 20% harvest of subadult and adult *C. rugosa* (CL ≥ 140 mm) is sustainable (Fig. 3; Table 2), even when extended or continuous periods of consecutive dry years occur (Fig. 4). Subsistence harvest rates as high as 30% are sustainable if harvest, owing to cultural responsibilities, occurs in only half of all possible dry years (Fig. 3). Therefore density-dependent hatchling survival, vital life-history traits (fast somatic growth and a small size of female maturity; Fordham *et al.* 2007a), and refugial years all play an important role in compensating subsistence harvests.

Our model projections indicate that the local persistence of many *C. rugosa* populations in northern tropical Australia is under severe threat owing to heavy predation by pigs. A conservative estimate of future pig predation (50% of turtles with CL > 100 mm predated each dry year (Fordham *et al.* 2006b, 2007a) resulted in turtle extirpation in <50 years (Fig. 2). The interaction between pig abundance and survival of *C. rugosa* is related to vegetation structure and timing of drying (Fordham *et al.* 2007a). Although dispersal rates of *C. rugosa* between woodland savanna billabongs are low (Fordham *et al.* 2006b, 2007a), local cyclonic activity and consecutive years of high rainfall induce rare episodes of interpopulation movement (D.A.F., unpublished data). Theoretically, spatial structure and population refugia could play a role in the persistence of pig-predated populations (McCullough 1996; Brook & Whitehead 2005b). However, dispersal-based

compensation from refugial sites would need to be extremely frequent to counter rapid population decline at sites where predation by pigs is common. Given that the magnitude and frequency of extreme flooding events is expected to rise in northern tropical Australia (Nott & Price 1999; Hughes 2003), *C. rugosa* may benefit from climate change via an increased frequency of inundation years and increased episodes of between-population movement. In the absence of any possible increase in recruitment through immigration, the frequency of refugial years would need to experience a fourfold increase to compensate pig predation rates ≥50% in dry years (Fig. 2).

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

The efficiency of headstarting turtles to mitigate the effects of adult mortality has been criticised (Frazer 1992) because management effort focused on increasing first-year turtle survival is perceived to be unlikely to promote population growth if subadult and adult survival remain low (Heppell, Crowder & Crouse 1996). Yet more recent evidence suggests that there is merit in efforts focused on increasing egg and hatchling survival (Dutton *et al.* 2005). We show that supplementing populations of freshwater turtles with additional yearlings provides a viable method to offset pig predation (Table 3), assuming that the survival of headstarted turtles is equivalent to those reared in the wild. Long-lived species with 'fast' recruitment that occupy relatively small, discrete, isolated populations, such as *C. rugosa*, are well suited to prosper from headstarting. Thus generating the number of additional yearlings needed for a positive impact on first-year survival in these *C. rugosa* populations (*N* < 300; Fordham 2007) is reasonably feasible (Table 3).

Unsustainably high levels of harvesting for human consumption are directly responsible for the precarious conservation status of many species of turtle (Klemens & Thorbjarnarson 1995; Gibbons *et al.* 2000). Nevertheless, if appropriate management institutions are implemented, harvesting long-lived reptiles can be sustainable (e.g. Bradshaw *et al.* 2006). For example, if turtle predation by pigs is minimized and subsistence harvesting is forfeited, commercial harvesting of adult and subadult *C. rugosa* (CL ≥ 140 mm) at an annual rate of 20% is sustainable, and a rate of 30% would not threaten persistence if harvesting occurred every second year (Fig. 3). Accordingly, an annual harvest quota of up to 30 turtles would not cause substantial population decline (see Results). Moreover, headstarting hatchlings could be used to increase harvest yields (Table 3). If managed correctly, the commercial harvest of subadult and adult *C. rugosa* could provide a rare example of a biologically sustainable turtle industry.

Our findings are of broad significance because they challenge the prevailing view that sustained subadult and adult survival is crucial for achieving long-term population stability in long-lived organisms (Musick 1999), and in particular freshwater turtles (Brooks, Brown & Galbraith 1991; Congdon *et al.* 1993, 1994; Cunnington & Brooks 1996; Heppell 1998; Converse, Iverson & Savidge 2005; Spencer & Thompson 2005). Furthermore, our research provides both empirical and predictive evidence to show the conservation threat that pigs pose to *C. rugosa*. Even conservative field estimates of pig-related turtle mortality (Fordham *et al.* 2007a) exceed what can be compensated by increased hatchling survival, and will assuredly lead to severe population declines.

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

Acknowledgements

References

Altman, J.C. (1982) Hunting buffalo in north-central Arnhem Land: a case study of rapid adaptation among aborigines. *Oceania*, **52**, 274–285.

Altman, J.C. (1984) The dietary utilisation of flora and fauna by contemporary hunter–gatherers at Momega outstation, north-central Arnhem Land. *Australian Aboriginal Studies*, **1984**, 35–46.

Altman, J.C. & Cochrane, M. (2005) Sustainable development in the indigenous-owned savannah: innovative institutional design for cooperative wildlife management. *Wildlife Research*, **32**, 473–480.

Bowman, M.J.S. & Robinson, C.J. (2002) The getting of the Nganabbarru: observations and reflections on aboriginal buffalo (*Bubalus bubalis*) hunting in Central Arnhem Land, Northern Australia. *Australian Geographer*, **33**, 191–206.

Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999) Seasonal compensation of predation and harvesting. *Oikos*, **87**, 419–426.

Bradshaw, C.J.A., Fuduka, Y., Letnic, M. & Brook, B.W. (2006) Incorporating known sources of uncertainty to determine precautionary harvests of saltwater crocodiles. *Ecological Applications*, **16**, 1436–1448.

Brook, B.W. & Bradshaw, C.J.A. (2006) Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, **87**, 1448–1451.

Brook, B.W. & Whitehead, P.J. (2005a) Plausible bounds for maximum rate of increase in magpie geese (*Anseranas semipalmata*): implications for harvest. *Wildlife Research*, **32**, 465–471.

Brook, B.W. & Whitehead, P.J. (2005b) Sustainable harvest regimes for magpie geese (*Anseranas semipalmata*) under spatial and temporal heterogeneity. *Wildlife Research*, **32**, 459–464.

Brook, B.W., Bowman, D.M.J.S., Bradshaw, C.J.A., Campbell, B.M. & Whitehead, P.J. (2006) Managing an endangered Asian bovid in an Australian national park: the role and limitations of ecological–economic models in decision-making. *Environmental Management*, **38**, 463–469.

Brooks, R.J., Brown, G.P. & Galbraith, D.A. (1991) Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). *Canadian Journal of Zoology*, **69**, 1314–1320.

Burnham, K.P. (1993) A theory for combined analysis of ring recovery and recapture data. *Marked Individuals in the Study of Bird Population* (eds J.D. Lebreton and P.M. North), pp. 199–213. Birkhauser-Verlag, Basel, Switzerland.

Caswell, H. (2001) *Matrix Population Models: Construction Analysis and Interpretation*, 2nd edn. Sinauer Associates, Sunderland, MA, USA.

Chaloupka, M. (2002) Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecological Modelling*, **148**, 79–109.

Chaloupka, M. (2004) Exploring the metapopulation dynamics of the southern Great Barrier Reef green turtle stock and possible consequences of sex-biased local harvesting. *Species Conservation and Management: Case Studies* (eds H. Akçakaya, M. Burgman, O. Kindvall *et al.*), pp. 340–354. Oxford University Press, New York.

Chaloupka, M. & Limpus, C. (2002) Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Marine Biology*, **140**, 267–277.

Close, L.M. & Seigel, R. (1997) Differences in body size among populations of red-eared sliders (*Trachemys scripta elegans*) subjected to different levels of harvesting. *Chelonian Conservation and Biology*, **2**, 563–566.

Cogger, H.G. (2000) *Reptiles and Amphibians of Australia*, 6th edn. Reed New Holland, Sydney.

Congdon, J.D., Dunham, A.E. & 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.

Congdon, J.D., Dunham, A.E. & van Loben Sels, R.C. (1994) Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist*, **34**, 397–408.

Converse, S.J., Iverson, B. & Savidge, J.A. (2005) Demographics of an ornate box turtle population experiencing minimal human-induced disturbance. *Ecological Applications*, **15**, 2171–2179.

Crouse, D.T., Crowder, L.B. & Caswell, H. (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, **68**, 1412–1423.

Cunnington, D.C. & Brooks, R.J. (1996) Bet-hedging theory and eigenelasticity: a comparison of the life histories of loggerhead sea turtles (*Caretta caretta*)

and snapping turtles (*Chelydra serpentina*). *Canadian Journal of Zoology*, **74**, 291–296.

Derocher, A.E., Lunn, N.J. & Stirling, I. (2004) Polar bears in a warming climate. *Integrative and Comparative Biology*, **44**, 163–178.

Doak, D., Kareiva, P. & Klepetka, B. (1994) Modelling population viability for the desert tortoise in the western Mojave desert. *Ecological Applications*, **43**, 446–460.

Dutton, D., Dutton, P., Chaloupka, M. & Boulon, R. (2005) Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biological Conservation*, **126**, 186–194.

Fordham, D. A. (2007) *Population regulation in snake-necked turtles in northern tropical Australia: modelling turtle population dynamics in support of Aboriginal harvests*. PhD. University of Canberra, Canberra.

Fordham, D., Georges, A. & Corey, B. (2006a) Compensation for inundation-induced embryonic diapause in a freshwater turtle: achieving predictability in the face of environmental stochasticity. *Functional Ecology*, **20**, 670–677.

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

Fordham, D.A., Georges, A. & Brook, B.W. (2007a) Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia. *Journal of Animal Ecology*, **76**, 1231–1243.

Fordham, D.A., Georges, A. & Corey, B. (2007b) Optimal conditions for egg storage, incubation and post-hatching growth for the freshwater turtle, *Chelodina rugosa*: science in support of an indigenous enterprise. *Aquaculture*, **270**, 105–114.

Fowler, C.W. (1987) A review of density dependence in populations of large mammals. *Current Mammalogy* (ed. H.H. Genways), pp. 401–441. Plenum Press, New York.

Frazer, N.B. (1992) Sea turtle conservation and halfway technology. *Conservation Biology*, **6**, 179–192.

Frazer, N.B. (2003) Prehistoric and ancient historic interactions between humans and marine turtles. *The Biology of Sea Turtles*, Vol. II (eds P. L. Lutz, J. Musick & J. Wyneken), pp. 1–38. CRC Press, Boca Raton, FL, USA.

Freckleton, R.P., Silva Matos, D.M., Bovi, M.L.A. & Watkinson, A.R. (2003) Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. *Journal of Applied Ecology*, **40**, 846–858.

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.

Georges, A. (1988) Sex determination is independent of incubation temperature in another chelid turtle, *Chelodina longicollis*. *Copeia*, **1988**, 248–254.

Georges, A. & McInnes, S. (1998) Temperature fails to influence hatchling sex in another genus and species of chelid turtle, *Elusor macrurus*. *Journal of Herpetology*, **32**, 596–598.

Georges, A., Guarino, F. & Bito, B. (2006) Freshwater turtles of the TransFly Region of Papua New Guinea – Notes on diversity, distribution, reproduction, harvest and trade. *Wildlife Research*, **33**, 373–384.

Gibbons, J.W., Scott, D.E., Ryan, T.J. *et al.* (2000) The global decline of reptiles, *déjà vu* amphibians. *Bioscience*, **50**, 653–666.

Heinsohn, R., Lacy, R.C., Lindenmayer, D.B., Marsh, H., Kwan, D. & Lawler, I.R. (2004) Unsustainable harvest of dugongs in Torres Straight and Cape York (Australia) waters: two case studies using population viability analysis. *Animal Conservation*, **7**, 417–425.

Heppell, S. (1998) Application of life-history theory and population model analysis to turtle conservation. *Copeia*, **1998**, 367–375.

Heppell, S.S., Crowder, L.B. & Crouse, D.T. (1996a) Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications*, **6**, 556–565.

Heppell, S.S., Limpus, C.J., Crouse, D.T., Frazer, N.B. & Crowder, L.B. (1996b) Population model analysis for the loggerhead sea turtle, *Caretta caretta*, in Queensland. *Wildlife Research*, **23**, 143–159.

Heppell, S.S., Caswell, H. & Crowder, L.B. (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, **81**, 654–665.

Hughes, L. (2003) Climate change and Australia: trends, projections and impacts. *Austral Ecology*, **28**, 423–443.

Hunter, C.M. & Caswell, H. (2005) Selective harvest of sooty shearwater chicks: effects on population dynamics and sustainability. *Journal of Animal Ecology*, **74**, 589–600.

Jackson, J.B., Kirby, M.X., Berger, W. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–637.

Jensen, A.L. (2000) Sex and age structured matrix model applied to harvesting a white tailed deer population. *Ecological Modelling*, **128**, 245–249.

Kennett, R. (1996) Growth models for two species of freshwater turtle, *Chelodina rugosa* and *Elseya dentata*, from the wet–dry tropics of northern Australia. *Herpetologica*, **52**, 383–395.

Kennett, R. & Christian, K. (1994) Metabolic depression in aestivating long-neck turtles (*Chelodina rugosa*). *Physiological Zoology*, **67**, 1087–1102.

Klemens, M.W. & Thorbjarnarson, J.B. (1995) Reptiles as food. *Biodiversity and Conservation*, **4**, 281–298.

Kokko, H. & Lindström, J. (1998) Seasonal density dependence, timing of mortality, and sustainable harvesting. *Ecological Modelling*, **110**, 293–304.

Marsh, H. (1996) Progress towards the sustainable use of dugongs by indigenous peoples in Queensland. *Sustainable Use of Wildlife by Aboriginal Peoples and Torres Straight Islanders* (eds M. Bomford & J. Caughley), pp. 139–151. Australian Government Publishing Service, Canberra.

McCarthy, M.A. (1996) Red Kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology*, **33**, 45–53.

McCarthy, M. & Thompson, C. (2001) Expected minimum population size as a measure of threat. *Animal Conservation*, **4**, 351–355.

McCullough, D.R. (1996) Spatial structured populations and harvest theory. *Journal of Wildlife Management*, **60**, 1–9.

Milner-Gulland, E.J., Shea, K., Possingham, H., Coulson, T. & Wilcox, C. (2001) Competing harvesting strategies in a simulated population under uncertainty. *Animal Conservation*, **4**, 157–167.

Musick, J.A. (1999) Ecology and conservation of long-lived marine animals. *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals*. American Fisheries Society Symposium 23 (ed. J.A. Musick), pp. 1–10. American Fisheries Society, Bethesda, MD, USA.

Musick, J.A., Burgess, G., Cailliet, G., Carmhi, M. & Fordham, S. (2000) Management of sharks and their relatives (Elasmobranchii). *Fisheries*, **25**, 9–13.

Nichols, J.D., Sauer, J.R., Pollock, K.H. & Hestbeck, J.B. (1992) Estimating transition probabilities for stage-based population matrices using capture-recapture data. *Ecology*, **73**, 306–312.

Nott, J. & Price, D. (1999) Waterfalls, floods and climate change: evidence from tropical Australia. *Earth and Planetary Science Letters*, **1999**, 267–276.

Pandolfi, J.M., Bradbury, R.H., Sala, E. *et al.* (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science*, **301**, 955–958.

R Development Core Team (2005) *A language and environment for statistical computing. Version 2·2·1 (December 2005 edn)*. R Foundation for Statistical Computing, Bristol, UK.

Rose, K.A., Cowan, J.H. Jr, Winemillere, K.O., Myers, R.A. & Hilborn, R. (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries*, **2**, 293–327.

Russell-Smith, J., Lucas, D., Gapindi, M. *et al.* (1997) Aboriginal resource utilization and fire management practice in Western Arnhem Land, monsoonal northern Australia: notes for prehistory, lessons for future. *Human Ecology*, **25**, 159–195.

Spencer, R.J. & Thompson, M.B. (2005) Experimental analysis of the impact of foxes on freshwater turtle populations. *Conservation Biology*, **19**, 845–854.

Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. *Journal of Marine Science*, **57**, 476–494.

Taylor, J. & Tulloch, D. (1985) Rainfall in the wet–dry tropics: extreme events at Darwin and similarities between years during the period 1870–1973. *Australian Journal of Ecology*, **10**, 281–295.

Taylor, M.K., Laake, J., McLoughlin, P.D. *et al.* (2005) Demography and viability of a hunted population of polar bears. *Arctic*, **58**, 203–214.

Tiwari, M., Bjorndal, K., Bolten, A. & Bolker, B. (2006) Evaluation of density-dependent processes and green turtle *Chelonia mydas* hatchling production at Tortuguero, Costa Rica. *Marine Ecology Progress Series*, **326**, 283–293.

Walker, T.I. (1998) Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research*, **49**, 553–572.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperilled species in the United States. *Bioscience*, **48**, 607–615.

Wisdom, M.J., Mills, L.S. & Doak, D. (2000) Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology*, **81**, 628–641.

Supplementary material

The following supplementary material is available for this article.

Fig. S1. Distribution of *Chelodina rugosa*.

This material is available as part of the online article from:

http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01414.x.
(This link will take you to the article abstract.)

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.