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

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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, hatching survival was density-dependent.

3. We show that field-based estimates of pig-related turtle mortality exceed levels that can be offset by increased hatching 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 hatching 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 hatching 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).
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 & Klepetskta 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 subsadult 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:

$$P = \frac{1 - \Phi_i^{d-1}}{1 - \Phi_i^{d}}, \quad \Phi_i = \left(1 - \frac{\Phi_i^{d-1}}{1 - \Phi_i^{d}} \right)$$

eqn 1
where $\Phi$ 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: $S_5$ represented mature males (CL = 140 mm). Female reproductive stages each had a fecundity rate ($F = 0.5 F_mak$ and $0.5 F_{mak}$). Egg mortality and hatching 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:

$$ A = \begin{pmatrix} P_1 & F_1 & F_4 & 0 & 0 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_5 & P_3 & 0 & 0 \\ 0 & 0 & G_4 & P_4 & 0 \\ 0 & 0 & F_1 & F_4 & P_5 \\ 0 & 0 & 0 & 0 & G_5 & P_6 \end{pmatrix} $$

### 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 = 180–220 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 hatching survival ($\Phi_0$). Clutch size is strongly correlated with body size (Fordham et al. 2007a). Mean clutch size for $S_3$ and $S_5$ 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)

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Percentage</th>
<th>Survival</th>
<th>Stage</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.930</td>
<td></td>
<td>0.0281</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.930</td>
<td></td>
<td>0.0281</td>
<td></td>
</tr>
<tr>
<td>Dry</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.834</td>
<td></td>
<td>0.037</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.834</td>
<td></td>
<td>0.037</td>
<td></td>
</tr>
<tr>
<td>Dry harvested</td>
<td>20</td>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.834</td>
<td>0.037</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.634</td>
<td>0.037</td>
</tr>
<tr>
<td>Dry harvested</td>
<td>30</td>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.834</td>
<td>0.037</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.534</td>
<td>0.037</td>
</tr>
<tr>
<td>Dry harvested</td>
<td>40</td>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.834</td>
<td>0.037</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.434</td>
<td>0.037</td>
</tr>
<tr>
<td>Dry pig predation</td>
<td>48</td>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.501</td>
<td>0.082</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.501</td>
<td>0.082</td>
</tr>
<tr>
<td>Dry pig predation</td>
<td>58</td>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.396</td>
<td>0.099</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.396</td>
<td>0.099</td>
</tr>
<tr>
<td>Dry pig predation</td>
<td>73</td>
<td>Juvenile</td>
<td>S1,5</td>
<td>0.24</td>
<td>0.069</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Adult</td>
<td>S2,4,6</td>
<td>0.24</td>
<td>0.069</td>
</tr>
</tbody>
</table>

$S_i$ and $S_s$ represent yearlings and 2-year-old juvenile females and males (carapace length, CL < 140 mm); $S_m$ subadult females (CL = 140–180 mm); $S_s$, small adult females (CL = 180–220 mm); $S_L$, large adult females (CL = 220 mm); $S_m$, mature males (CL = 140 mm). Mortality due to subsistence harvest by people is additive, whereas pig predation is partly compensatory.
Φ₀ was derived as the number of hatchlings that hatch (H) divided by the number subsequently alive after one year (H₀). *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 hatching production owing to our decision to set effective clutch frequency to one. H was calculated using the equation:

\[ H = [(N_1 \times m_1 \times r) + (N_4 \times m_4 \times r)] \times h \]  

(eqn 3)

**DENSITY DEPENDENCE**

Hatching 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 Inimbar and Gimmilly billabongs, and live recapture and dead recovery (Burnham Models; Burnham 1993) analysis prior to and after a rare harvest event at Murryullulkul, allowed hatching survival (Φ₀) to be estimated when population size (N) was at 32% (Φ₀ = 0·30), 43% (Φ₀ = 0·10), 78% (Φ₀ = 0·14) and 100% (Φ₀ = 0·01) of estimated carrying capacity (Fordham 2007; Fordham et al. 2007a). Hatching survival at very low densities (1%) was assumed to be high (Φ₀ = 0·93; Table 1). The relationship between density and log survival was strongly linear (r² = 0·936) and thus a linear density dependent decay function was used to model the relationship between Φ₀ and N:

\[ Φ₀ = a \times \exp(b \times N) \]  

(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 hatching recruitment declines. This affects the realized population growth rate by negatively influencing Fₙ and F₄.

**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 Giddedella, in years of high pig abundance, occurred at an estimated rate of 48% of S₄ (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 Dambam, pig predation was estimated to be 38% (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 Murrybuljuluk, 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 S₁ turtles were varied by sampling parameters from a uniform distribution with ranges of 1–1·4 years; 1·6–2·2 years for S₂; 3·5–5·1 years for S₃; and 1·6–1·9 years for S₄ (based on Fordham et al. 2007a). Survival estimates for wet years were likewise varied between Φ₅ₚ = 0·783–0·977; Φ₄ₚ = 0·746–0·895 for dry years with no harvest or pig predation; Φ₃ₚ = 0·134–0·784 for dry years with pig predation; Φ₂₃ₖ = 0·39–0·48; and Φ₁ₜ = 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 S1, S2 and S3) 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 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).

**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

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Percentage</th>
<th>EP</th>
<th>EMS</th>
<th>Population decrease (%)</th>
<th>Median population size</th>
</tr>
</thead>
<tbody>
<tr>
<td>No harvest and no pig predation</td>
<td>0.000</td>
<td>**</td>
<td>**</td>
<td></td>
<td>185 (136–235)</td>
</tr>
<tr>
<td>Pig predation</td>
<td>20</td>
<td>0.000</td>
<td>91</td>
<td></td>
<td>107 (85–157)</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.000</td>
<td>11</td>
<td></td>
<td>34 (14–99)</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>1.000</td>
<td>0</td>
<td></td>
<td>11 (7–33)</td>
</tr>
<tr>
<td>Customary harvest every dry year</td>
<td>20</td>
<td>0.000</td>
<td>84</td>
<td></td>
<td>100 (73–147)</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.298</td>
<td>24</td>
<td></td>
<td>50 (16–107)</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>0.982</td>
<td>0</td>
<td></td>
<td>16 (9–53)</td>
</tr>
<tr>
<td>Customary harvest in 50% of dry years</td>
<td>20</td>
<td>0.000</td>
<td>97</td>
<td></td>
<td>144 (100–203)</td>
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<td>30</td>
<td>0.000</td>
<td>75</td>
<td></td>
<td>118 (65–189)</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>0.108</td>
<td>42</td>
<td></td>
<td>87 (20–174)</td>
</tr>
<tr>
<td>Annual commercial harvest</td>
<td>20</td>
<td>0.000</td>
<td>82</td>
<td></td>
<td>90 (69–109)</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.395</td>
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<td>32 (14–61)</td>
</tr>
<tr>
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<td>40</td>
<td>0.996</td>
<td>0</td>
<td></td>
<td>11 (8–16)</td>
</tr>
<tr>
<td>Commercial harvest every second year</td>
<td>20</td>
<td>0.000</td>
<td>95</td>
<td></td>
<td>129 (92–180)</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.017</td>
<td>62</td>
<td></td>
<td>96 (45–160)</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>0.353</td>
<td>25</td>
<td></td>
<td>60 (14–138)</td>
</tr>
</tbody>
</table>

**Population size increased. Extinction 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.

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 needed 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 hatching 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.
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.

...tropical northern Australia (Fordham et al. 2007a). However, dispersal-based structure and population refugia could play a role in the movement (D.A.F., unpublished data). Theoretically, spatial et al. between woodland savanna billabongs are low (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 hatching 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).

![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).](image-url)
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

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References

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:

(This link will take you to the article abstract.)

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