

# Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia

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## Summary

1. Species that mature late, experience high levels of survival and have long generation times are more vulnerable to chronic increases in mortality than species with higher fecundity and more rapid turnover of generations.
2. Many chelonians have low hatchling survival, slow growth, delayed sexual maturity and high subadult and adult survival. This constrains their ability to respond quickly to increases in adult mortality from harvesting or habitat alteration. In contrast, the northern snake-necked turtle *Chelodina rugosa* (Ogilby 1890) is fast-growing, early maturing and highly fecund relative to other turtles, and may be resilient to increased mortality.
3. Here we provide correlative evidence spanning six study sites and three field seasons, indicating that *C. rugosa* is able to compensate demographically to conditions of relatively low subadult and adult survival, caused by pig *Sus scrofa* (Linnaeus 1758) predation and customary harvesting by humans.
4. Recruitment and age specific fecundity tended to be greater in sites with low adult and subadult survival (and thus reduced densities of large turtles), owing to higher juvenile survival, a smaller size at onset of maturity and faster post-maturity growth.
5. These patterns are consistent with compensatory density-dependent responses, and as such challenge the generality that high subadult and adult survival is crucial for achieving long-term population stability in long-lived vertebrates such as chelonians.
6. We posit that long-lived species with 'fast' recruitment and a capacity for a compensatory demographic response, similar to *C. rugosa*, may be able to persist in the face of occasional or sustained adult harvest without inevitably threatening population viability.

*Key-words:* age-specific fecundity, capture–mark–recapture, Chelidae, compensation, density dependence, juvenile recruitment, population regulation, survival, wildlife utilization.

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## Introduction

Density-dependent processes appear to regulate the abundance of a wide range of organisms (Brook & Bradshaw 2006). Such processes compensate for sporadic reductions in density, providing resilience by assisting population recovery after downward displacement of population numbers (Sinclair & Pech

1996), even in long-lived reptiles such as *Crocodylus porosus* (Bradshaw *et al.* 2006). The same compensatory processes that provide resilience to perturbation also afford resistance to chronic depression of abundance. For example, downward pressure on bird abundance by harvest can be resisted by dynamic adjustment of survival or fecundity (Nichols *et al.* 1984). Similarly, compensatory mechanisms are thought to enhance persistence of some reptile populations during periods of reduced survival (Massot *et al.* 1992), but there have been few comprehensive studies addressing explicitly these demographic issues in chelonians. Studies to date (Stubbs *et al.* 1985;

Brooks, Brown & Galbraith 1991; Bjørndal, Bolten & Chaloupka 2000; Tiwari *et al.* 2006) have been limited by: (i) lack of appropriate replication; (ii) focus upon a compensatory shift in a single demographic parameter (such as juvenile growth and its interaction with age of maturity) rather than an assessment of all potential compensatory responses; and (iii) the use of indirect evidence of differential survival probabilities such as levels of habitat disturbance rather than direct measures of survival.

Life history traits of long-lived vertebrates constrain the ability of populations to respond to chronic increases in mortality (Heppell, Caswell & Crowder 2000) because compensatory responses are thought to be limited and recovery is slow (Musick *et al.* 2000). Among amniotes, turtles characteristically have a life history strategy of high fecundity accompanied by low egg and hatchling survival, slow growth, late maturity and high juvenile and adult survival (Heppell 1998; Chaloupka & Limpus 2002). Thus turtles are viewed typically as having 'slow' life histories, and as such harvesting the small fraction of individuals that survive the vulnerable early life history stages may jeopardize population persistence, because these individuals have high reproductive potential (Cunnington & Brooks 1996; Heppell *et al.* 1996). However, a universal perception on freshwater turtle vulnerability to harvest, based on deterministic models (Congdon, Dunham & van Loben Sels 1993, 1994), should be interpreted with considerable care (Mills, Doak & Wisdom 1999). A 'slow-fast' continuum in life histories exists for a range of taxa, including mammals (Heppell *et al.* 2000), birds (Saether, Ringsby & Røskaft 1996), reptiles (Webb, Brook & Shine 2002) and sharks (Smith, Au & Show 1998), and a species position along this continuum influences how population growth will respond to change in a demographic trait (Saether & Bakke 2000). It may be that high rates of survival are crucial for some turtle species (Brooks *et al.* 1991; Chaloupka 2002), while the life history traits and population dynamics of other species may better equip them to compensate some level of increased mortality through predation or harvest, as is the case with chondrichthyans (Stevens *et al.* 2000).

Traits that contribute heavily to population growth in long-lived vertebrates, such as adult survival, tend to be buffered against changes in population density or stochastic factors (Pfister 1998). Traits such as juvenile survival and somatic growth contribute proportionately less to population growth, but are more sensitive to variation in density because they are commonly constrained by intraspecific competition (Fowler 1987; Gaillard, Festa-Bianchet & Yoccoz 1998). Today, as in the past, wild populations of subadult and adult turtles are commonly harvested for both subsistence and commercial purposes (Gibbons *et al.* 2000; Georges, Guarino & Bito 2006). Some marine turtle populations may compensate for decreased abundance by adjusting life history parameters, such as somatic growth or

fecundity, as a response to reduced density (Bjørndal *et al.* 2000; Tiwari *et al.* 2006), but the prevailing perception is that freshwater turtles do not display density-dependent responses in reproductive effort, recruitment or somatic growth (Brooks *et al.* 1991). According to this view, fixed demographic parameters constrain the ability of freshwater turtle populations to recover following population depression and limit their ability to respond to a chronic increase in adult mortality, whether it be direct through harvesting, or indirect through habitat alteration (Converse, Iverson & Savaidge 2005). Thus the harvest of adult turtles at almost any level is often regarded as inherently unsustainable, and therefore unacceptable (Congdon *et al.* 1993, 1994).

Population resilience in the presence of intermittent harvest is particularly relevant to the northern snake-necked turtle *Chelodina rugosa* (Ogilby 1890). It is a fast-growing, early-maturing and highly fecund species in comparison with many other turtles (Kennett 1996, 1999). It attains high densities in the ephemeral swamps and other wetlands of the wet-dry tropics of northern Australia. Turtle activity is punctuated each year by the dry season, when the wetlands draw down and often completely dry. Immediately before drying, turtles move to the shallows, bury in the mud and aestivate (Kennett & Christian 1994). Historically, aestivating *C. rugosa* provided a source of protein for indigenous communities living on, or near, ephemeral wetlands (Russell-Smith *et al.* 1997). Today, harvest rates by humans are negligible primarily because pigs *Sus scrofa* (Linnaeus 1758), an exotic predator, deplete stocks immediately before harvesting is possible (Fordham *et al.* 2006b). Rainfall in the wet-dry tropics is highly variable, both within and across years, in the quantity that falls and its timing (Taylor & Tulloch 1985). In unusually wet years billabongs (large waterholes) do not dry, turtles do not aestivate, and thus harvesting and pig predation is limited. These refugial years are potentially important for local population persistence of *C. rugosa* (Fordham *et al.* 2006b).

In this paper, we examine variation in demographic parameters in *Chelodina rugosa* across waterholes subject to varying levels of harvest and pig predation. We interpret the correlations as indicative of compensatory demographic responses in *C. rugosa*, a turtle species with relatively 'fast' life history traits, assisting this species to persist in the face of chronic low adult and subadult survival caused by pig predation and Aboriginal harvesting.

## Materials and methods

### STUDY LOCATION AND EXPERIMENTAL DESIGN

Six discrete populations of *C. rugosa* were studied in central Arnhem Land, Northern Territory, Australia,

from 2002 until 2006. Billabongs were selected to be representative of the variation in frequency of drying and frequency of harvest. Two of the six populations, Giddadella (12°31'29"S; 134°21'01"E) and Damdam (12°09'50"S; 134°37'36"E), dried annually and were subject to harvesting at least once per year during the period of study (except in 2004, when Damdam was closed to harvesters for ritual purposes). A further two populations, Murrybulljuluk (12°37'34"S; 134°50'47"E) and Little-Giddadella (12°30'49"S; 134°21'38"E), dried annually but were rarely harvested because of their relative isolation or historical pattern of use. Little-Giddadella had no record of harvest. Murrybulljuluk was harvested in 2003, an event that had not occurred for at least 15 years prior (Otto Bulmaniya Campion, personal communications). The remaining two populations, Imimbar (12°43'51"S; 134°31'50"E) and Ginmilly (12°19'11"S; 134°30'08"E) typically do not dry in any year and are therefore unharvested. Pig predation was not controlled as part of the experimental design as the influence of pigs was not appreciated until the work was under way. Level of pig predation was incorporated as an uncontrolled covariate. These six populations were used to compare key demographic parameters, such as survival, juvenile recruitment, growth, fecundity and size of maturity, and to determine their correlation with billabong permanence, harvest regime and feral pig abundance. The interaction between survival, harvest and pigs was calculated using the entire data set (2002–06), while all other demographic traits were calculated using data collected only in 2003 and 2004. This was necessary because only the dry seasons of 2002 and 2003 offered environmental conditions suitable to the experimental design. All six populations were located at least 1.5 km from the nearest water body. *C. rugosa* do not migrate when discrete waterholes dry (Fordham *et al.* 2006b), although a low level of dispersal occurs during rare flooding events (Fordham, unpublished data). As such, the location of each population ensured that emigration and immigration were sufficiently low so as not to invalidate our demographic analysis.

#### TRAPPING AND MEASUREMENT PROCEDURES

Each population was trapped twice per year from 2002 to 2005. In 2005 Damdam and Murrybulljuluk dried earlier than usual, which restricted trapping, while in 2006 turtles were caught only once at the end of the wet season. The methodology used to capture and mark turtles; measure turtle size and weight; sex and age turtles; estimate size of maturity, female reproductive activity and clutch frequency; determine clutch size relative to body size; and to class turtles as either hatchlings, juveniles, subadults or adults, is described in detail in Appendix S1 (see Supplementary material).

#### MODELLING GROWTH

Growth rates were estimated from annual capture data (captures before drying or at the end of the dry season: September–October). Growth rate was calculated as the incremental difference in carapace length (CL) divided by the number of years between captures. Von Bertalanffy, Gompertz and logistic curves were fitted to growth data separately for male and female turtles at each population (Frazer, Whitfield Gibbons & Greene 1990) implemented in PROC NLIN in SAS version 8 (SAS Institute 2001). The von Bertalanffy model had the smallest residual mean square (degrees of freedom equal across models) and hence was the model used. The age–size relationship was calculated using the equation:

$$\text{Age} = \frac{\ln [1 - (h/a)] - \ln [-(Lr/a) + 1]}{k} \quad \text{eqn 1}$$

where  $h$  = CL at hatching (mm),  $a$  = asymptotic CL (mm),  $Lr$  = CL (mm) and  $k$  = growth parameter. Size at hatching equalled mean *C. rugosa* hatching size (carapace length = 33.28 mm,  $n = 135$ ; Fordham, unpublished data). Bootstrapping was used to estimate the standard error and 95% confidence limits for age. While we acknowledge that least-squares approaches have been criticized (Ratkowsky 1986; James 1992), independent age estimates derived from examination of plastral annuli accorded with age estimates using the maximum likelihood estimation (MLE) approach for male and female turtles up to a size of maturity in all six populations, thus indicating that the potential biases from the MLE approach had been adequately contained.

#### ABORIGINAL HARVEST

Harvest data were typically collected directly during harvest events. When we were unable to accompany harvesters, community members at Kolorbidahdah, Damdam and Wurdeja outstations (settlements where the majority of harvesters reside) were asked to store the shells of turtles harvested at Giddadella and Damdam, leading to unmeasured underestimation in the true harvest rate (Fordham *et al.* 2006b). Communities in the near vicinity of the two seasonal, but rarely harvested billabongs, were contacted regularly during the harvest season to determine whether harvesters had visited these billabongs. The size and sex of harvested turtles was also recorded, when possible, to assess whether Aboriginal people display a size or sex bias in turtles that are selected for harvest.

#### PIG ROOTING AND ABUNDANCE

Pig rooting (soil disturbance caused by digging for food items) was used as an indicator of pig abundance (Hone 1988). Pigs congregate at billabongs as they draw down, dispersing shortly after the billabong dries

(Fordham *et al.* 2006b). Thus, pig rooting was measured only at billabongs that draw down and dry annually, estimated from data collected 2–4 weeks after drying. Transects were established for each compass quarter (north, south, east and west) by laying a tape from the centre of the billabong (site of the last remaining water) to the maximum perimeter. Pig rooting was estimated as a percentage disturbance directly under the tape for each alternate 10-m interval. Pig rooting was classed as severe if percentage rooted exceeded 20% and minimal if less than 20%.

#### MODELLING SURVIVAL

Program MARK version 4.2 (Colorado State University; White & Burnham 1999) was used to estimate *C. rugosa* survival ( $\phi$ ) and recapture probabilities ( $p$ ). The joint analysis of live and dead encounters of marked animals as described by Burnham (1993), which include an estimate of recovery rates ( $r$ ) and site fidelity ( $f$ ), was used to estimate  $\phi$  and  $p$  at regularly drying billabongs. The advantage of this modelling approach has been demonstrated for turtle populations (Bjørndal, Bolten & Chaloupka 2003). Data on turtle mortalities were obtained by regularly circumnavigating all billabongs before and during drying, by accompanying harvesters on harvest activities and by surveying communities that lie within a close proximity of harvested billabongs. Recovery rates met the assumption of the Burnham model; there was no substantive bias in the recovery of dead turtles from different mortality sources (Francis & Cooke 1993). Site fidelity was fixed to 1 (100%), because (i) emigration and immigration were minimal owing to choice of study site (discrete, distant billabongs) and (ii) *C. rugosa* tend to aestivate rather than move in response to the periodic absence of water (Fordham *et al.* 2006b). The standard Cormack–Jolly–Seber recaptures-only method was used to model survival at rarely drying billabongs because dead recoveries were rare or non-existent.

Two candidate model sets were formulated in program MARK before analysis: one for seasonal billabongs and another for rarely drying billabongs. Akaike's information criterion, corrected for small sample size ( $AIC_c$ ), was used as an objective means of model selection (Burnham & Anderson 2001). Turtle CL was modelled as an individual covariate. Turtles with carapace lengths < 140 mm (juveniles) and  $\geq$  140 mm (adult males and subadult and adult females) were considered grouped factors (levels). Where trapping period varied from the standard 20-day period, a relative index of trapping period, averaged across all individuals in the population, was modelled as an across-population covariate. In addition, the presence or absence of water, harvest and the monsoonal rains were treated as cofactors, as was the severity of pig rooting.

The candidate model set was used to test whether periodic absence of water, pig abundance and harvest determine turtle survival and recapture probabilities

and whether size is an important covariate. We hypothesized (a priori) that survival would decline markedly in response to harvest and pig abundance and that size would influence survival positively in populations where negative perturbations in abundance are rare. Survival and recapture probabilities were model-averaged using Akaike weights ( $w_i$ ) to include model uncertainty in the estimates of parameter precision (Burnham, Burnham & Augustin 1997). The importance of individual covariates in the models constrained the available goodness-of-fit tests (Telfer *et al.* 2002). Goodness-of-fit was evaluated by comparing the deviance of the explanatory models with reference to the deviance of the null model. In each case the saturated model explained greater than 74% of the deviance, and thus adequate model fit was concluded. Recapture probabilities were used to calculate population abundance using the Horvitz–Thompson type estimator [ $N_i = (n_i/p_i)$ ; Seber (1982)], where  $n_i$  is the number of turtles captured,  $p_i$  is the estimated recapture probability and  $N_i$  is estimated population abundance in the  $i$ th year. Approximate 95% confidence intervals were derived from the model-averaged standard error (SE) of  $p_i$  based on a normal approximation, whereby  $p_i \pm (1.96 \times SE)$  was substituted in the Horvitz–Thompson equation given above.

#### STATISTICAL ANALYSIS

The R statistical package version 2.1.1 (R Development Core Team 2005) was used to assess the statistical relationships between population variation in gravid turtle size, clutch size and post-maturity growth. Bootstrapping, where data were sampled repeatedly with replacement (10 000 times), was used to estimate the standard error and confidence intervals via the percentile method (Crawley 2002). Generalized linear models (GLM) were used to test whether clutch size or mass varied with population of origin (population) or covaried with survival probability between years (high/low; survival). Clutch size and clutch mass in *C. rugosa* is correlated positively with female body size (Kennett 1999), and thus CL (size) was treated as a covariate in the analysis.

The statistical evidence for correlations between recruitment and survival, proportion of small reproductively active females (CL = 180–200 mm) and survival, and female post-maturity growth and survival were evaluated by an evidence ratio approach using Akaike weights. Binomial GLM models [equivalent to analysis of variance (ANOVA) and analysis of covariance (ANCOVA)] with logit-link functions were used to determine the statistical relationship between recruitment (hatchlings present/absent; *hatchling*), small females (proportion of gravid turtles greater or less than 25%; gravid) and female post-maturity (CL  $\geq$  220 mm) growth (greater or less than 3 mm/year; *growth*), and: (i) population of origin; (ii) survival probability; and (iii) billabong type (annually dry, harvested, pig-impacted/

rarely dry, unharvested, rarely pig-impacted/rarely dry, unharvested, rarely pig-impacted; *billabong type*).

## Results

### ABORIGINAL HARVEST

Aboriginal harvests were attempted at Giddadella in 2002 [number taken ( $n$ ) = 13 turtles], 2003 ( $n$  = 10), 2004 ( $n$  = 8) and 2005 ( $n$  = 0) and at Damdam in 2002 ( $n$  = 38), 2003 ( $n$  = 14) and 2005 ( $n$  = 0) and Murrybulljuluk in 2003 ( $n$  = 38). Note that harvesters did not capture any turtles in 2005 at either of the two seasonal, regularly harvested billabongs, despite attempting harvests. The size distribution of harvested turtles included only adults and subadults (carapace length  $\geq 140$  mm; see Supplementary material, Fig. S1).

### SURVIVAL ANALYSIS

#### *Annually dry, harvested, pig-impacted billabongs*

According to the most parsimonious survival model for Giddadella, severity of pig rooting had the largest influence on survival ( $\phi$ ) and recapture probabilities ( $p$ ), while recovery rates ( $r$ ) were influenced by the presence or absence of water and turtle size (Table 1; see Table S1 for entire model set). A second acceptable model, ranked lower but not substantially so, modelled  $\phi$  and  $p$  as a factor of turtle size as well as severity of pig rooting (Table 1). There was weaker support for the next ranked model, which had  $\phi$  and  $p$  driven by water presence or absence rather than pig rooting (Table 1). Turtle harvesting was attempted at least once during

each drying period, and as such, harvest could not be disentangled from drying *per se*. In any case, the relative lack of support for this third model indicates that severity of rooting has a greater influence over  $\phi$  and  $p$  at Giddadella than harvest. Model-averaged survival probabilities (weighted by  $AIC_c$  support) were relatively high [ $\phi$  = 0.708; 95% confidence intervals (CI) = 0.591–0.802] when rooting was low or absent, and shifted in a negative direction in response to severe rooting ( $\phi$  = 0.503; CI = 0.250–0.761; Fig. 1).

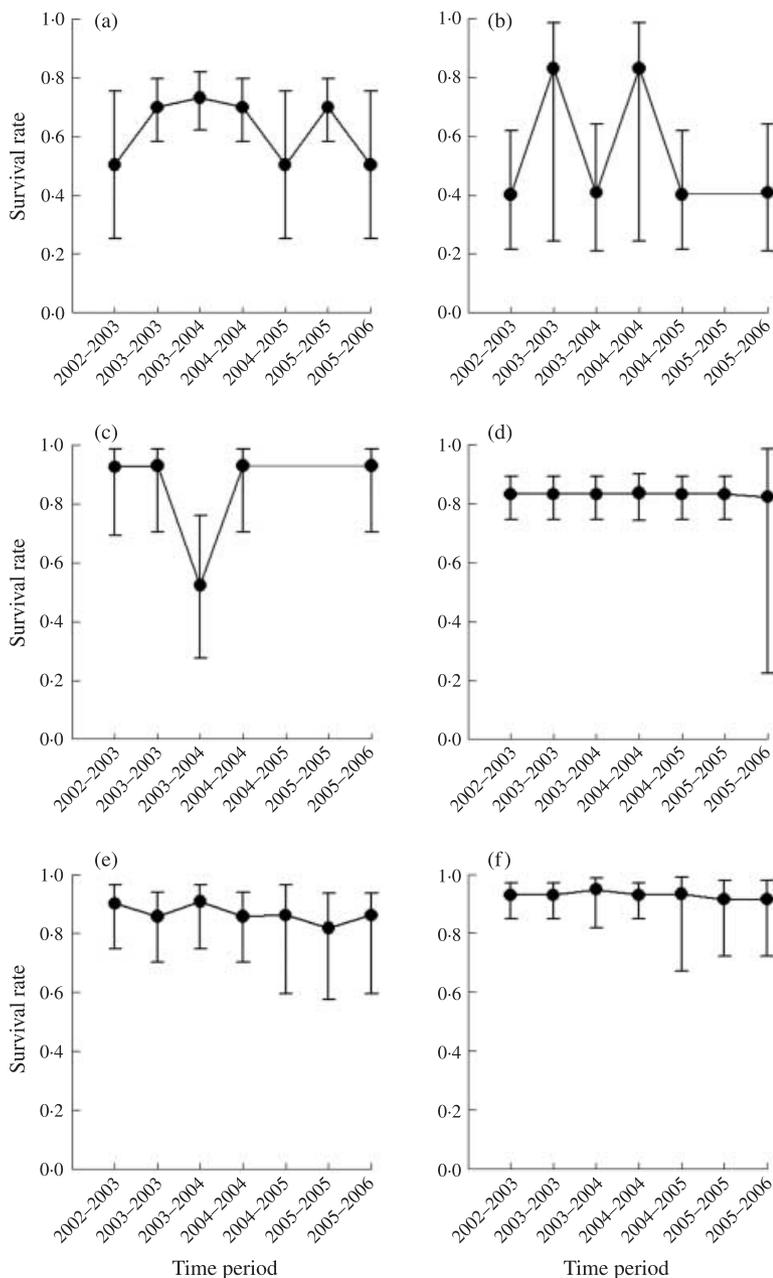
The best-supported survival model at Damdam modelled  $\phi$ ,  $p$  and  $r$  as dependent upon the presence or absence of water, while turtle size positively influenced  $r$  (Table 1). Two similar models, each modelling  $\phi$ ,  $p$  and  $r$  as a factor of the presence or absence of water, received some degree of support (Table 1). Pig rooting was severe during each drying period at Damdam, and as such, the influence of pig rooting on  $\phi$  and  $p$  could not be disentangled from drying *per se*. There was little support for modelling  $\phi$  and  $p$  as a direct factor of harvest (see Supplementary material, Table S1) suggesting that, as at Giddadella, harvest did not noticeably influence  $\phi$  and  $p$  at Damdam. Mean model averaged survival probabilities at Damdam were high between periods of inundation ( $\phi$  = 0.831; CI = 0.25–0.986), responding negatively to drying ( $\phi$  = 0.396; CI = 0.203–0.629; Fig. 1).

#### *Annually dry, rarely harvested or pig-impacted billabongs*

According to the most parsimonious model at Murrybulljuluk, a rare harvest event, at the end of 2003, had the greatest influence over  $\phi$  and  $p$ , while  $r$  was

**Table 1.** Burnham–Both mark–recapture model set, showing Akaike's information criterion ( $AIC_c$ ), number of parameters ( $k$ ), deviance (Dev), change in  $AIC_c$  compared to the best-ranked model ( $\Delta AIC_c$ ) and model weights ( $w_i$ ), for Giddadella (a), Damdam (b), Murrybulljuluk (c) and Little-Giddadella (d). Turtle size ( $s$ ) was modelled as a covariate. Juvenile turtles (size < 140 mm) and adult and subadult turtles (size  $\geq 140$  mm) were grouped and treated as a grouped factor ( $g$ ). The presence or absence of water ( $wtr$ ) and harvesting ( $h$ ) were treated as cofactors, as was severity of pig rooting ( $rt$ ). Where necessary, a relative index of trapping period ( $t$ ) averaged across all individuals in the population was modelled as an across-population covariate. A time constant ( $\cdot$ ) was also modelled. Note that only models with  $w_i > 0.05$  are shown (see Table S1 in Supplementary material for the complete model set)

Site	Model	$AIC_c$	$k$	Dev	$\Delta AIC_c$	$w_i$
a	$\phi(rt)p(rt^+t)r(wtr^+s)f(I)$	900.82	9	882.377	0	0.418
	$\phi(rt^+s)p(rt^+s^+t)r(wtr^+s)f(I)$	902.503	11	879.851	1.68	0.18
	$\phi(wtr)p(wtr^+t)r(wtr^+s)f(I)$	903.095	9	884.653	2.28	0.134
	$\phi(rt)p(rt^+t)r(wtr)f(I)$	903.421	8	887.068	2.6	0.114
b	$\phi(wtr)p(wtr)r(wtr^+s)f(I)$	498.952	8	482.441	0	0.413
	$\phi(wtr^+g)p(wtr^+g)r(wtr^+s)f(I)$	500.197	12	475.075	1.24	0.222
	$\phi(wtr)p(wtr)r(wtr)f(I)$	500.796	7	486.4	1.84	0.164
	$\phi(wtr^+g)p(wtr^+g)r(wtr)f(I)$	502.913	11	479.967	3.96	0.057
c	$\phi(h)p(h)r(wtr^+s)f(I)$	282.156	8	265.196	0	0.648
	$\phi(h^+s)p(h^+s)r(wtr^+s)f(I)$	284.802	10	263.316	2.65	0.173
	$\phi(h^+g)p(h^+g)r(wtr^+s)f(I)$	285.471	12	259.334	3.32	0.124
d	$\phi(rt)p(rt)r(wtr)f(I)$	281.43	7	266.568	0	0.558
	$\phi(rt)p(rt)r(wtr^+s)f(I)$	282.761	8	265.644	1.33	0.287
	$\phi(rt^+s)p(rt^+s)r(wtr)f(I)$	285.956	9	266.549	4.53	0.058



**Fig. 1.** Model-averaged survival probabilities for turtles at Giddadella (a) and Damdam (b) (annually dry, harvested), Murrybulljuluk (c) and Little-Giddadella (d) (annually dry, rarely harvested), Imimbar (e) and Ginnilly (f) (rarely dry, not harvested). Note that survival at Damdam and Murrybulljuluk in 2005 could not be estimated because the billabong dried earlier than usual (see Methods).

influenced by the presence or absence of water and turtle size (Table 1). There was less support for the next ranked model, which modelled  $\phi$  and  $p$  as a factor of size as well as harvest (Table 1). Mean model-averaged survival probabilities were high in the absence of harvest ( $\phi = 0.929$ ; CI = 0.700–0.986), responding negatively to harvest ( $\phi = 0.524$ ; CI = 0.276–0.76; Fig. 1). At Little-Giddadella, the most parsimonious model established that  $\phi$  and  $p$  were dependent upon the severity of pig rooting, while the presence or absence of water influenced recovery rates (Table 1). A second model,

similar in structure to the first but with a size effect on  $r$ , was also well supported (Table 1). Mean model-averaged survival probabilities at Little-Giddadella were high in the absence of heavy rooting ( $\phi = 0.833$ ; CI = 0.746–0.895; Fig. 1).

#### *Rarely dry, unharvested, rarely pig-impacted billabongs*

The most parsimonious survival model at Imimbar modelled  $\phi$  and  $p$  as dependent upon turtle size (Table 2; see Supplementary material, Table S2 for entire model set). A model ranked lower, but not substantially so, modelled  $\phi$  and  $p$  as a factor of the monsoonal rains, as well as turtle size (Table 2). The mean model-averaged survival probability at Imimbar was 0.867 (CI = 0.667–0.949; Fig. 1). Similarly, the best-supported model at Ginnilly modelled  $\phi$  and  $p$  as dependent upon turtle size (Table 2). There was considerably less support for the next-ranked model, which modelled  $\phi$  and  $p$  as a factor of the monsoonal rains, as well as size (Table 2). The mean model-averaged survival probability at Ginnilly was 0.929 (CI = 0.783–0.977; Fig. 1).

## DEMOGRAPHIC CORRELATIONS

### *Juvenile recruitment*

Hatchlings and juveniles were proportionately common in populations that experienced low adult survival during 2002–04 (Table 3). In contrast, hatchlings and juveniles were proportionately rare in populations with high adult survival (Table 3). Notably, at Murrybulljuluk, hatchlings were absent in 2003, while in 2004, following a rare negative perturbation in density caused by harvest, hatchlings were common (Table 3).

Hatchling recruitment was correlated strongly with the survival estimates, suggesting that hatchling recruitment increases as a response to reduction in overall population density. The most parsimonious model had the presence or absence of hatchlings as a function of survival probability ( $hatchling = survival$ ;  $w_i = 0.843$ ). There was little support for the models  $hatchling = population$  ( $\Delta_i = 4.17$ ;  $w_i = 0.102$ ),  $hatchling = billabong\ type$  ( $\Delta_i = 5.83$ ;  $w_i = 0.044$ ), the null model ( $\Delta_i = 7.22$ ;  $w_i = 0.022$ ) or the global model ( $\Delta_i = 8.03$ ;  $w_i = 0.015$ ). As such, the survival model had 38 times greater support from the data than did the null, based on the ratio of their respective Akaike weights.

### *Size of maturity*

Minimum size of maturity for female *C. rugosa* was 182.5 mm (range = 160.4–188.2 mm;  $n = 448$ ) and 147.9 mm for males (range = 139.9–151.9 mm;  $n = 343$ ). Small female turtles (CL = 180–200 mm) tended to be gravid during the peak of the breeding season in populations that experienced frequent periods of low survival (Giddadella and Damdam; Fig. 2). In contrast,

**Table 2.** Cormack–Jolly–Seber mark–recapture model set showing Akaike’s information criterion ( $AIC_c$ ), number of parameters ( $k$ ), deviance ( $Dev$ ), change in  $AIC_c$  compared to the best-ranked model ( $\Delta AIC_c$ ) and model weights ( $w_i$ ), for Imimbar (a) and Ginmilly (b). Turtle size ( $s$ ) was modelled as a covariate. Juvenile turtles (size < 140 mm) and adult and subadult turtles (size  $\geq$  140 mm) were grouped and treated as a grouped factor ( $g$ ). The presence or absence of monsoonal rains ( $mr$ ) was treated as cofactors. A relative index of trapping period ( $t$ ) averaged across all individuals in the population was modelled as an across-population covariate. A time constant model (.) was also modelled. Note that only models with  $w_i > 0.05$  are shown (see Table S2 in Supplementary material for the complete model set)

Site	Model	$AIC_c$	$k$	$Dev$	$\Delta AIC_c$	$w_i$
a	$\phi(s)p(s^+t)$	729.446	5	719.251	0	0.639
	$\phi(mr^+s)p(mr^+s^+t)$	730.989	7	716.621	1.54	0.295
b	$\phi(s)p(s^+t)$	226.825	5	216.102	0	0.748
	$\phi(mr^+s)p(mr^+s^+t)$	229.052	7	213.0669	2.23	0.246

females in populations with high constant survival (Imimbar and Ginmilly) or rare periods of reduced survival (Murrybulljuluk and Little-Giddadella) tended not to breed until reaching a larger size (CL > 200 mm; Fig. 2). Median gravid turtle size at Murrybulljuluk in 2003 (251.1 mm; CI = 236.9–265.0) and 2004 (248.7 mm; CI = 233.6–263.1) remained constant despite a rare negative population perturbation late in 2003 caused by harvesting.

The proportion of small gravid females correlated with the survival estimates. The most parsimonious model had the proportion of small gravid females as a function of survival probability ( $gravid = survival$ ;  $w_i = 0.718$ ). There was little support for the models  $gravid = population$  ( $\Delta_i = 3.19$ ;  $w_i = 0.145$ ),  $gravid = billabong\ type$  ( $\Delta_i = 4.29$ ;  $w_i = 0.084$ ), the null model ( $\Delta_i = 5.49$ ;  $w_i = 0.046$ ) or the global model ( $\Delta_i = 9.60$ ;  $w_i = 0.006$ ). As such, the survival model had 16 times greater support from the data than did the null. A

tendency for smaller females to be gravid in populations that frequently experience depressed survival suggests that size of maturity may be influenced by density.

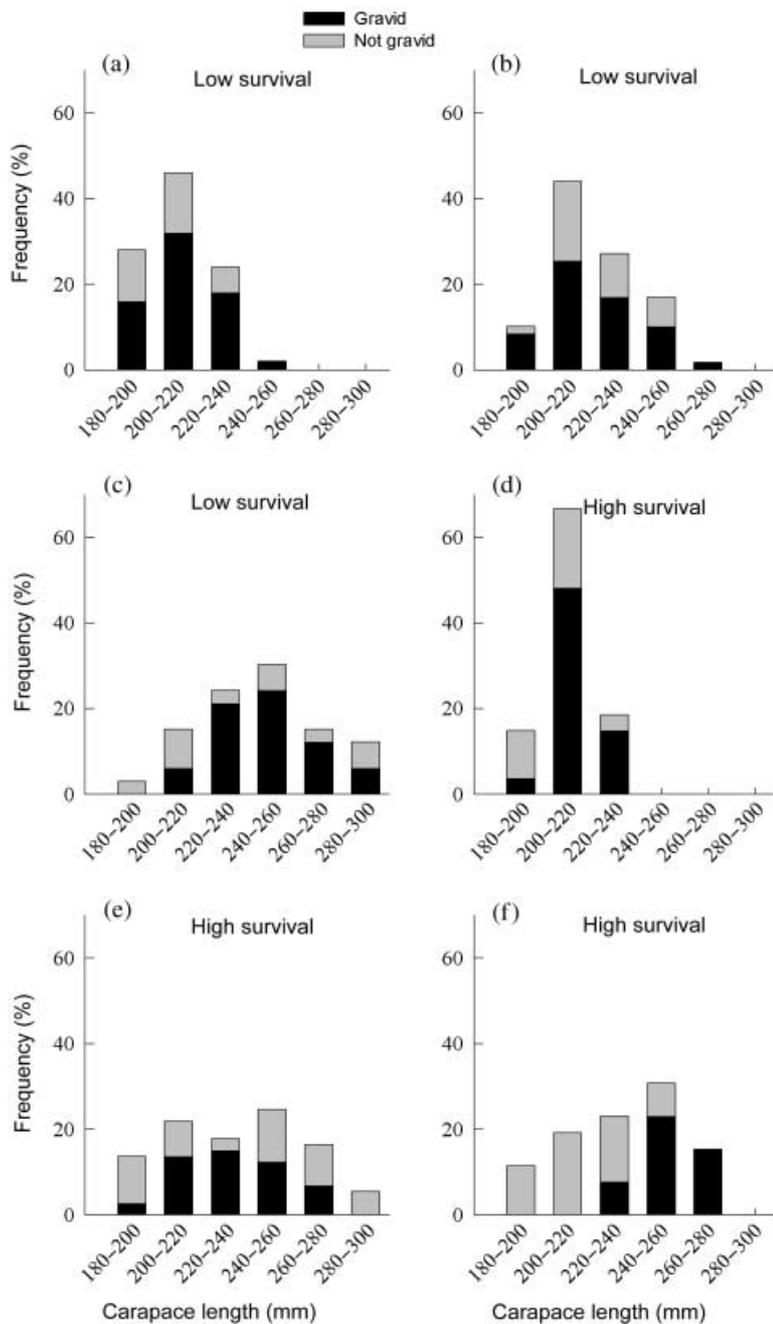
#### Growth and age of maturity

With the exception of turtles at Damdam, predicted age at onset of female maturity (CL = 182.5 mm) was similar in populations that had recently experienced periods of low survival (Giddadella and Murrybulljuluk) to populations with high survival (Little-Giddadella, Imimbar, Ginmilly; see Supplementary material, Table S3). At Damdam predicted growth from hatching to minimum size of maturity was just 3.3 years (CI = 3.0–3.5). Mature female growth (CL > 220 mm) tended to be faster in populations that experienced periods of low adult survival during 2002–04 than most populations that experienced high survival (Fig. 3). At Damdam and Giddadella mature female growth was fast and survival low, with turtles rarely surviving to asymptotic size (see Supplementary material, Table S3). Survival probability had the largest influence on female post-maturity growth, suggesting a density-dependent compensatory response in somatic growth rates. The most parsimonious model had female post-maturity growth as a function of survival probability ( $growth = survival$ ;  $w_i = 0.735$ ). There was little support for the models  $growth = population$  ( $\Delta_i = 2.77$ ;  $w_i = 0.183$ ),  $growth = billabong\ type$  ( $\Delta_i = 4.50$ ;  $w_i = 0.077$ ), and no support for the global model ( $\Delta_i = 11.00$ ;  $w_i = 0.003$ ) or the null model ( $\Delta_i = 12.63$ ;  $w_i = 0.001$ ). Indeed, the survival model in this case had > 700 times more support from the data than did the null.

Male growth rates were independent of survival estimate; there was no correlation between survival estimate and age at onset of male maturity (see Supplementary material, Table S3). Although mature males

**Table 3.** Horvitz–Thompson population abundance estimates for hatchlings, juveniles and total population size at Giddadella (a), Damdam (b), Murrybulljuluk (c), Little-Giddadella (d), Imimbar (e) and Ginmilly (f). Approximate 95% confidence intervals are in parenthesis (see Methods)

Site	Billabong type	Survival 2002–2004	Hatchlings	Juveniles	Total abundance
2003					
a	Annually dry, harvested	Periodically low	32 (24–53)	8 (6–13)	164 (118–267)
b	Annually dry, harvested	Periodically low	22 (14–48)	7 (5–16)	165 (107–372)
c	Annually dry, rarely harvested	Periodically low	0	14 (9–27)	173 (116–331)
d	Annually dry, rarely harvested	High	0	0	34 (29–42)
e	Rarely dry, unharvested	High	0	8 (6–13)	331 (237–547)
f	Rarely dry, unharvested	High	0	0	51 (37–81)
2004					
a	Annually dry, harvested	Periodically low	28 (22–38)	22 (17–30)	125 (99–169)
b	Annually dry, harvested	Periodically low	14 (9–29)	10 (7–22)	147 (96–312)
c	Annually dry, rarely harvested	Periodically low	62 (42–119)	0	179 (121–345)
d	Annually dry, rarely harvested	High	0	2 (1–2)	32 (28–40)
e	Rarely dry, unharvested	High	7 (6–9)	0	243 (201–307)
f	Rarely dry, unharvested	High	0	0	59 (44–87)

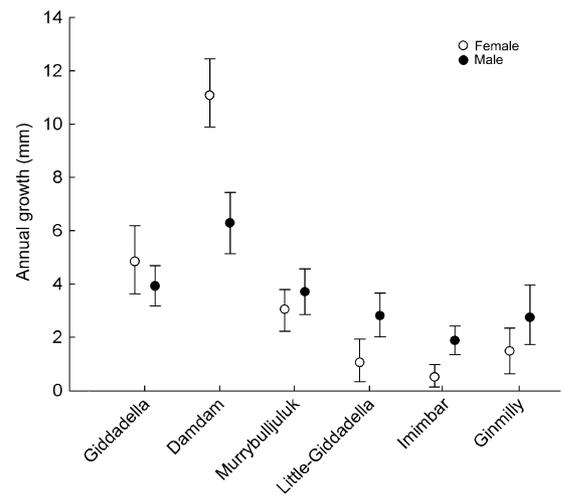


**Fig. 2.** Reproductive status of female turtles during peak-breeding season. With the exception of Murrybulljuluk (c), small turtles (< 200 mm) tended to be gravid at populations, such as Giddadella (a) and Damdam (b), which experienced periodic low survival during 2002–04. In contrast, turtles tended not to reproduce until reaching a larger size (> 200 mm) at Little-Giddadella (d), Imimbar (e) and Ginnilly (f), populations that experienced high survival.

(CL = 148 mm) grew faster at Damdam, male post-maturity growth did not correlate with reduced survival (Fig. 3).

#### Fecundity

Clutch size was strongly positively correlated with body size. Based on the evidence ratio (ER, ratio of  $w_i$  between two models), the linear model was  $1.35 \times 10^{19}$



**Fig. 3.** Mean post-maturity growth rates (mm/year) for females > 220 mm and males  $\geq$  148 mm. Mature female growth tended to be faster in populations that experienced periods of low adult survival during 2002–04 (Giddadella, Damdam, Murrybulljuluk).

times better supported by the data than the null model. Clutch size did not correlate with survival probability. The most parsimonious model had clutch size as a function of population of origin and body size ( $clutch = population + size$ ;  $w_i = 0.624$ ). There was little support for the global model ( $\Delta_i = 2.31$ ;  $w_i = 0.197$ ) and the models  $clutch = survival + size$  ( $\Delta_i = 3.06$ ;  $w_i = 0.135$ ), and  $clutch = size$  ( $\Delta_i = 5.33$ ;  $w_i = 0.043$ ). There was no support for the null model ( $\Delta_i = 23.94$ ;  $w_i < 0.001$ ). The most parsimonious model for clutch mass was  $mass = survival + size$  ( $w_i = 0.531$ ). A second acceptable model, ranked lower, but not substantially so, was  $mass = population + size$  ( $\Delta_i = 1.66$ ;  $w_i = 0.232$ ). There was little support for the global model ( $\Delta_i = 2.26$ ;  $w_i = 0.171$ ) and the model  $mass = size$  ( $\Delta_i = 4.19$ ;  $w_i = 0.065$ ), and no support for the null model ( $\Delta_i = 54.64$ ;  $w_i < 0.001$ ). Turtles in populations with high and low survival tended to lay three to four clutches annually, although in some years turtles probably laid only two clutches, while in other years turtles may have laid up to five clutches (see Supplementary material, Table S4).

#### Discussion

Density-dependent processes are a pervasive feature of the population dynamics of most organisms (Rose *et al.* 2001; Brook & Bradshaw 2006), but the degree to which they can compensate for chronic increases in mortality, especially in long-lived taxa, remains unclear (Pöysä *et al.* 2004). The harvesting of freshwater turtles has been widely criticized because their life history attributes and population dynamics are thought to make them particularly vulnerable to off-take (Cunnington & Brooks 1996; Heppell 1998). In particular they have been presumed to be unable to respond to harvest through density-dependent

compensatory processes (Congdon *et al.* 1993, 1994). Life history traits may directly influence population persistence under conditions of reduced survival caused by harvest (Smith *et al.* 1998). Species that mature late, experience high levels of survival and have long generation times are more vulnerable to over-exploitation than species with higher fecundity and more rapid turnover of generations (Musick 1999). *C. rugosa* is fast-growing, highly fecund and early-maturing compared to other turtles (Kennett 1996, 1999) making *C. rugosa* better suited to cope with frequent episodes of low survival than chelonians that have been studied previously. Moreover, our analysis suggests strongly that *C. rugosa* has the capacity to compensate for low rates of adult survival via increases in juvenile survival, decreases in size of maturity and increases in post-maturity growth; in turn promoting an increase in juvenile recruitment and age-specific fecundity.

An interaction between density and juvenile survival has been established for birds (Sedinger, Lindberg & Chelgren 2001), mammals (Fowler 1987; Gaillard *et al.* 1998), reptiles (Massot *et al.* 1992) and fish (Rose *et al.* 2001). At high densities, the survival of small individuals may be depressed owing to low per capita resource availability during reproduction (Choquenot 1991), or increased resource competition after birth or hatching (Sedinger *et al.* 1998). Alternatively, cannibalism (adults eating their young) can result in strong density-dependent feedback in juvenile survival, as documented in a variety of fish species (Rose *et al.* 2001). In *C. rugosa*, low subadult and adult survival appears to elicit greater hatchling survival and in turn greater juvenile recruitment. Hatchlings and juveniles (CL < 140 mm) were well represented at populations that experienced episodes of low survival during 2002–04 (Giddadella, Damdam and Murrybulljuluk), compared to those that experienced relatively higher probabilities of survival (Little-Giddadella, Imimbar and Gimilly; Table 3). Juvenile abundance provides a good proxy for hatchling recruitment (Madsen & Shine 2000), particularly given that turtle mortality at harvested billabongs was not size-dependent in *C. rugosa*. Furthermore size influenced *C. rugosa* survival positively at rarely drying billabongs (populations with high overall survival; Table 2). This finding is consistent with the hypothesis that *C. rugosa* populations are regulated by density, which influences negatively the recruitment of small individuals into the larger size classes.

A density-dependent interaction between somatic growth, body condition and age-specific fecundity may arise when animal size or nutritional status, rather than age, dictate maturity (Jorgenson *et al.* 1993; Festa-Bianchet, Gaillard & Jorgenson 1998). Alternatively, increasing age-specific fecundity in response to low survival may result from a decrease in size of maturity (Abrams & Rowe 1996). Small, gravid turtles (carapace length < 200 mm) were relatively common during peak-breeding season in populations that frequently

experience periods of low survival (Giddadella and Damdam) compared to populations where survival remained high (Fig. 2). In maturing at a smaller size in populations with low survival, age-specific fecundity is increased without a concomitant increase in juvenile and subadult growth. Because female reproductive size at Murrybulljuluk did not decline in response to a rare period of low survival in 2003 (see Results), decreased size of maturity may be a local adaptation – an evolved response that promotes demographic resilience, and therefore persistence, under conditions of comparatively low survival (Bronikowski & Arnold 1999; Olsen *et al.* 2004). To clarify this assertion, manipulative studies are needed to test experimentally the processes that promote a reduction in size of maturity in response to reduced survivorship.

In populations with relatively high survival probabilities, *C. rugosa* growth is typical of many long-lived vertebrates (e.g. Frazer *et al.* 1990; Miguel & Cubillos 2006). Growth is rapid to maturity, whereupon growth becomes slow and indeterminate (Kennett 1996). In contrast, females in populations with low survival continue to grow vigorously after reaching maturity (Fig. 3). Clutch size is often related directly to age or body size in birds and reptiles (Massot *et al.* 1992; Sedinger *et al.* 1998), including *C. rugosa* (see Results); thus, a fast rate of post-maturity growth increases age-specific fecundity in response to reduced survival. Post-maturity growth in males, who invest relatively fewer resources in reproduction, is not influenced strongly by population survival probabilities (Fig. 3). Although long-lived organisms often display a strong positive relationship between survival and body size or age (e.g. Heppell 1998), size does not enhance *C. rugosa* survival under conditions of high pig predation and harvest (Table 1). Hence, a compensatory increase in age-specific fecundity is the only plausible explanation for accelerated female post-maturity growth in populations where survival probabilities are low.

The number of offspring responds to density (Sedinger *et al.* 1998), and reproductive frequency may influence population growth in some long-lived organisms (Bradshaw, Mollet & Meekan 2007). Clutch size and mass may decline with increasing density in reptiles (Massot *et al.* 1992), although this was not the case for *C. rugosa*. Although clutch size was influenced strongly by site of capture, neither clutch size nor clutch mass were influenced strongly by survival probability. Annual reproductive frequency did not vary with survival, but remained high compared to freshwater turtles (e.g. Congdon *et al.* 1993, 1994) and other long-lived vertebrates [e.g. sharks (Cortès 2002)], potentially promoting resistance to depressions in abundance; turtles tended to produce three to four clutches each year, irrespective of survival probabilities (see Supplementary material, Table S4).

Humans commonly mediate changes in the abundance of chelonians (Gibbons *et al.* 2000), yet density dependence in vital rates has often been regarded as

unimportant (e.g. Doak *et al.* 1994; Chaloupka 2002), although there are exceptions (e.g. Tiwari *et al.* 2006). Our correlative analysis indicates that the life history traits and population dynamics of *C. rugosa* allow compensation of some level of increased mortality; and chelonians, like condrichthyans (Smith *et al.* 1998; Stevens *et al.* 2000), have differential vulnerabilities to human impacts such as harvesting, habitat destruction and invasive species. Pig abundance had the largest impact on *C. rugosa* survival. The strongest compensatory response, indicated by the correlation analysis, occurred in populations where pig abundance was high and thus rooting severe (Damdam and Giddadella). These populations were distinguished by high juvenile recruitment, early onset of maturity and fast post-maturity growth. Harvest rates were low at sites where pig abundance was high. Harvesting immediately before, and during, the early aestivation period, when pig predation is high, provided an improved harvest yield in the face of this predator competition. Only 35 years ago, *C. rugosa* yields were relatively high in Arnhem Land [study region (Russell-Smith *et al.* 1997)] and pigs were, in all probability, locally rare or non-existent, because pig meat was consumed rarely (Altman 1984). We infer that turtle harvesting would have been compensated at least partially through density-dependent responses. Harvesting in 2003 at Murrybulljuluk, where pig abundance is low, caused a marked decline in turtle survival (Fig. 1), which correlated with greater hatchling recruitment in 2004 (Table 3), signalling a compensatory response to harvest.

The interaction between pig abundance and *C. rugosa* survival is complex, being related to prominent vegetation type [presence or absence of *Eleocharis*, a seasonal dietary staple for pigs (Fordham *et al.* 2006b)] and timing of drying. Although spatial refugia could, theoretically, play an important role in regulating pig-predated populations (McCullough 1996), *C. rugosa* dispersal rates between woodland savannah billabongs are low (Fordham *et al.* 2006b), restricting such regulation. In contrast, refugial years, caused by variation in seasonal rainfall (Fordham *et al.* 2006a), may be important for population persistence. In 2003 Giddadella dried later than in previous years (i.e. November, rather than June–August), forcing pigs to congregate around more permanent water sources, leading to low pig abundance, high consequent turtle survival (Fig. 1) and, thus, extension of the compensatory mortality period. Conversely, in 2005 Little-Giddadella dried earlier than usual (August rather than November–December), causing high pig abundance, negatively impacting turtle survival.

To our knowledge, this is the first replicated study to demonstrate comprehensively a correlation between demographic parameters and variation in subadult and adult survival in a turtle species. The significance of these findings are broad, challenging the prevailing view that sustained high post-hatchling survival is

crucial for achieving long-term population stability in chelonians (Brooks *et al.* 1991; Congdon *et al.* 1993, 1994; Doak, Kareiva & Klepetka 1994; Heppell *et al.* 1996; Heppell 1998; Chaloupka 2002; Converse *et al.* 2005). Our capture–mark–recapture evidence suggests that chelonians with life history traits similar to *C. rugosa* may persist periods of low post-hatchling survival via a range of density-dependent compensatory responses. Rock art and ceremonial stories indicate that *C. rugosa* populations have survived many millennia of traditional harvesting (Chaloupka 1993), and it is reasonable to assume that compensatory strategies such as those described in this paper are responsible for population persistence in *C. rugosa* over this long period of interaction with humans in tropical northern Australia.

Although survival probabilities that varied across billabongs provided an opportunity to infer density-dependent compensatory responses in *C. rugosa*, there are limitations to inferring causality from correlation. There remains a need to demonstrate density-dependent responses conclusively, ideally through experimental manipulations of population size.

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## Supplementary material

The following supplementary material is available for this article.

**Appendix S1.** Detailed trapping and measurement procedures.

**Fig. S1.** Pooled size distribution of harvested turtles (a) and trapped turtles (b) at Giddadella, Damdam and Murrybulljuluk billabongs. Harvesting by indigenous people targets subadult and adult turtles (carapace length  $\geq 140$  mm).

**Table S1.** Entire Burnham–Both mark–recapture model set showing Akaike’s Information Criterion (AIC<sub>c</sub>), number of parameters ( $k$ ), deviance (Dev), change in AIC<sub>c</sub> compared to the best-ranked model ( $\Delta$ AIC<sub>c</sub>) and model weights ( $w_i$ ), for Giddadella (a), Damdam (b), Murrybulljuluk (c), Little-Giddadella (d). See Table 1 for a description of model variables.

**Table S2.** Entire Cormack–Jolly–Seber mark–recapture model set showing Akaike’s information criterion (AIC<sub>c</sub>), number of parameters ( $k$ ), deviance (Dev), change in AIC<sub>c</sub> compared to the best-ranked model ( $\Delta$ AIC<sub>c</sub>) and model weights ( $w_i$ ), for Imimbar (a) and Ginmilly (b). See Table 2 for a description of model variables.

**Table S3.** von Bertalanffy growth parameter ( $k$ ), asymptotic size, age of maturity, post-maturity growth and percentage of turtles caught of asymptotic size at Giddadella (a), Damdam (b), Murrybulljuluk (c), Little-Giddadella (d), Imimbar (e) and Ginmilly (f). Note that female post-maturity growth is calculated using growth data from females with CL  $\geq$  220 mm, while female age of maturity is based on minimum size of maturity (182.5 mm). Male post-maturity growth and age of maturity is calculated using minimum size of male maturity (CL = 148 mm).

**Table S4.** Seasonal occurrence of corpora lutea and ovarian follicles of various sizes for *Chelodina rugosa* at Giddadella (a), Damdam (b), Murrybulljuluk (c),

Little-Giddadella (d), Imimbar (e) and Ginmilly (f). Potential clutches are highlighted in yellow. Note that turtles in populations with high and low survival tended to lay three to four clutches annually.

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