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Experimental evidence for density-dependent responses to mortality of snake-necked turtles

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Abstract Density-dependent compensation has rarely been demonstrated in long-lived vertebrates in highly variable environments, such as the wet–dry tropics, where complex factors impact on vital rates. We used an experimental manipulation of population density in six replicated wild populations of the northern snake-necked turtle (*Chelodina rugosa*). We show that this species can rebound rapidly following reductions in density, and so is resilient to harvest and predation by pigs. Remarkably, in some populations, turtle abundance took as little as 1 year to recover from a strong negative perturbation (>50% experimental population reduction) in adult density. This was achieved through an increase in hatchling recruitment and survival into larger size classes. Our manipulative experiments, viewed concomitantly with previous experimental and correlative research, challenge the general perceptions that freshwater turtles universally are highly susceptible to any form of off-take and that high sub-adult and adult survival is crucial for achieving long-term population stability in freshwater turtles generally. In the case of *C. rugosa*, such generalities would produce overly cautious prescriptions for sustainable management.

Keywords Chelidae · Population manipulation · Population regulation · Juvenile recruitment · Wildlife utilization

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Introduction

Density-dependent processes provide resilience for populations to recover rapidly from a downward perturbation of population numbers (Bradshaw et al. 2006), and resistance to chronic depressions of abundance (Nichols et al. 1984), in a wide range of organisms (Brook and Bradshaw 2006). Long-lived species are typically viewed as having "slow" life histories (slow growth, delayed maturity and high survival), which constrain the resilience of their populations to exploitation (Musick 1999). This is because their compensatory responses are thought to be limited and recovery slow (Musick et al. 2000; Smith et al. 1998). However, some long-lived vertebrates compensate for increases in mortality through increased natural survival or fecundity, owing to reduced intraspecific competition (Fowler 1987; Gaillard et al. 1998). A "slow–fast" continuum in life histories exists for mammals (Heppell et al. 2000), birds (Saether et al. 1996) and reptiles (Webb et al. 2002), and a species position along this continuum influences the sensitivity of population growth to changes in key demographic parameters (Saether and Bakke 2000). Thus, the life history traits, ecology and population dynamics of some long-lived vertebrates are better equipped to compensate a level of increased mortality through predation or harvest (Fordham et al. 2007).

The prevailing perception is that density-dependent responses are weak or non-existent in freshwater turtles (Brooks et al. 1991; Congdon et al. 1993, 1994), owing to life history strategies characterized by high fecundity (compared to other amniotes), low hatchling survival, delayed maturity, high juvenile and adult survival, and potentially long lifespans (Heppell 1998). As such, harvesting adult and sub-adult turtles is thought to jeopardize population persistence, because it is the older individuals that have the highest reproductive value (Congdon et al. 1993, 1994; Cunnington and Brooks 1996). Although high rates of survival are certainly crucial for the persistence of some chelonians (Chaloupka 2002; Doak et al. 1994; Heppell 1998) the generality of this statement has been challenged for turtles (Fordham et al. 2007) and other long-lived organisms, such as chondrichthyans, which exhibit differential vulnerability to exploitation (Stevens et al. 2000; Walker 1998). Work on multiple populations of the northern snake-necked turtle *Chelodina rugosa* Ogilby 1890 has established a correlation between the intensity of sub-adult and adult turtle mortality (caused by pig *Sus scrofa* Linnaeus 1758 predation and indigenous harvesting) and key life history parameters. These correlations indicate that *C. rugosa* may compensate for low rates of sub-adult and adult survival via: (1) increases in hatchling survival, (2) decreases in female size at maturity, and (3) increases in female post-maturity growth (Fordham et al. 2007).

The ephemeral swamps and other wetlands of the wet–dry tropics of northern Australia support high densities of *C. rugosa*. Turtle activity is punctuated each year by the dry season, when the wetlands gradually lose water and often completely dry. Immediately before drying, turtles move to the shallows, bury in the mud and aestivate (Kennett and Christian 1994). Pigs prey heavily on *C. rugosa* during this period, killing a large proportion of the inactive turtles (Fordham et al. 2006b), reducing turtle abundance, possibly prompting a density-dependent response (Fordham et al. 2007). Although correlative analyses suggest that a fast-growing, early-maturing and highly fecund species like *C. rugosa* may be well equipped to compensate for relatively high levels of adult mortality (Fordham et al. 2007), manipulative studies are needed to confirm causation (Cappuccino and Harrison 1996).

How populations respond to disturbance that displaces them from their equilibrium abundance is of wide interest to ecologists (Sibly et al. 2007) and of fundamental importance to the conservation and management of species subjected to human impacts such as exploitation. However, the interaction between population growth and extrinsic and intrinsic factors, such as climatic variability and demographic structure, makes quantifying density-dependent responses (in population growth and individual vital rates) difficult (Clutton-Brock and Coulson 2002; Lande et al. 2006). Without

sufficient replicated experimentation, it is not usually possible to separate density-dependent compensation from fortuitous recovery (e.g., owing to favorable environmental conditions) following harvest mortality even in well-studied species (Pöysä et al. 2004). Manipulation of population size or other ecological variables such as predation pressure provides one way to establish the presence or absence of density-dependent responses (Sinclair et al. 2006). Field perturbation experiments (and correlative approaches; Gaillard et al. 2000) have overwhelmingly focused on long-lived taxa in relatively stable climates and ecologically less complex systems (e.g., Stewart et al. 2005). Yet, the exploitation of potentially long-lived organisms is severe in less stable environments, such as the wet–dry tropics (e.g., Brook and Whitehead 2005), where complex factors impact on vital rates (Fordham et al. 2008). Thus our ability to use a scientific approach to manage these ecologically, economically and socially important species is severely limited. Approaches by Kennett (1994) (who manipulated *C. rugosa* density in a downward direction) and Fordham et al. (2007) (who monitored a population prior to, and after, a closely scrutinized harvest event) provide rare examples of mechanistic research in highly variable systems; and strongly suggest that *C. rugosa* population regulation is, at least partially, dependent on population abundance.

In this study, by manipulating population size (via reduction and supplementation), we explore experimentally the demographic processes which underlie population regulation in *C. rugosa*; a potentially long-lived vertebrate distributed in a complex system where multiple variable factors influence vital rates (Fordham et al. 2008). While recognizing that previous correlative and manipulative evidence is supportive of density-dependent regulation (Fordham et al. 2007; Kennett 1994), here we adopt a more categorical approach, using a replicated (spatial and temporal) experimental framework to investigate the relative importance of density-dependent processes in driving the dynamics of *C. rugosa*. We use demographic data collected prior to manipulation at six previously studied populations (2003–2004; Fordham et al. 2007), providing post-manipulation estimates of key life history traits (2005–2006) using new field data. Specifically we test whether *C. rugosa* populations are regulated by a density-dependent response in: (1) turtle survival, (2) hatchling recruitment and subsequent survival into larger size classes, (3) female post-maturity growth, and (4) reproductive size.

Materials and methods

Study location and experimental design

Seven discrete isolated billabong (waterhole) populations of *C. rugosa* were studied in central Arnhem Land, Northern

Territory, Australia, from 2002 until 2006. They are referred to by their Aboriginal names. The location, regularity of drying and harvest history of six of the seven populations is described elsewhere (Fordham et al. 2007). The location of the additional population, Garromgarrom (12°18.6′S; 134°29.5′E), typically does not dry in any year and therefore is unharvested.

During January and February 2005, the densities of three populations (Imimbar, Ginmilly and Garromgarrom) were reduced and the captured animals were used to supplement the populations in Giddadella and Damdam. It is often difficult to achieve exact replicated levels of manipulation in the field (Pedersen et al. 2004): manipulated populations were either reduced by 50–70% or supplemented by 80–100%. Reduction and supplementation involved only adult and sub-adult turtles [carapace length (CL) > 140 mm] because only large individuals tend to be harvested by people (e.g., Fordham et al. 2006b; Georges et al. 2006). The numbers of turtles removed at Imimbar, Ginmilly and Garromgarrom were 142, 40 and 27 (58%, 68% and 64% of the population) respectively (S1). Giddadella was supplemented with 97 turtles, while Damdam was supplemented with 146, causing a 98% and 81% increase in population size, respectively (S1). Turtles from an additional billabong, Jibenna (12°9′S; 134°30′E), were used to cover the shortfall in supplement animals. Murrybulljuluk and Little-Giddadella were chosen as controls and were not manipulated (see below for summary of treatments). In 2005 (i.e., after manipulating reduced and supplement populations), turtle abundance at Little-Giddadella was reduced by an unanticipated depression in adult survival brought about by predation by pigs, a rare event for this waterhole (Fordham et al. 2007), thus we regarded Little-Giddadella as an unconstrained treatment (S1).

The experimental design allowed key demographic parameters to be compared prior to (2003–2004; based on Fordham et al. 2007) and after (2005–2006) density manipulation. Despite the formidable logistical constraints involved with manipulating remote natural systems, we were able to achieve some level of spatial and temporal control. The location of each population ensured that emigration and immigration were sufficiently low so as not to invalidate our demographic analysis (Fordham et al. 2007).

Trapping and measurement procedures

Each population was trapped twice per year, from 2002 to 2005 (Fordham et al. 2007). In 2005, an additional trapping session, at the beginning of the wet season, was undertaken at manipulated billabongs. In 2006 all populations were trapped from May to June (14–17 months after manipulation). The methodology of Fordham et al. (2007) was used to measure turtle size, sex turtles, estimate female reproductive activity and distinguish hatchlings, yearlings and 2-year juveniles.

Turtle survival and density

Program Mark 4.2 (Colorado State University; White and Burnham 1999) was used to estimate *C. rugosa* survival (ϕ) and recapture probabilities (p) using live-recaptures-only models and combined live-recaptures and dead-recoveries models (Burnham models; Burnham 1993). A candidate set of survival and recapture models (2002–2006) for all populations except Garromgarrom was previously used to investigate the impact of environmental (e.g., rainfall) and human-driven factors (e.g., harvest rates and feral pig abundance; Fordham et al. 2007). An identical live-recaptures-only candidate model set was created for Garromgarrom (S2). Akaike's information criterion weights (w_i), whereby model support is scaled between 0 and 1 relative to all models under consideration, was used as an objective means of model comparison for these survival models (Burnham and Anderson 2001). To test the strength of evidence that manipulation influences the survival of individuals remaining at each experimental population—working from an established basis that complex factors impact on survival rates—manipulation was modeled as a single-term model and as an additive factor to the most parsimonious model concluded from prior analysis (Fordham et al. 2007; S3); models with little information-theoretic support ($w_i < 0.05$) were excluded from the new candidate set.

Survival and recapture probabilities were model-averaged using w_i, so as to include model selection uncertainty in the estimates of parameter precision (Buckland et al. 1997). Recapture probabilities were used to calculate population abundance and approximate 95% confidence intervals (CI) using the standard Horvitz-Thompson estimator ($N_i = n_i/p_i$; Seber 1982) and following methods described by Fordham et al. (2007). ArcView GIS 3.2 software was used to calculate the surface area of each billabong from perimeter location points taken at the end of each wet season. Population density was calculated as number of individuals per hectare.

Female post-maturity growth

Female post-maturity growth in body size was calculated as the incremental difference in CL divided by the number of years between captures. Bootstrapping was used to estimate CI via the percentile method (Crawley 2002) using the *R* statistical package version 2.1.1 (R Development Core Team 2005).

Generalized linear mixed-effects models

Binomial generalized linear mixed-effects models, with logit-link functions and population of origin (site) as a random effect, were used to determine the statistical relationship between: (1) the total proportion of hatchlings

and yearlings in the population, and (2) the proportion of reproducing small (CL = 180–200 mm) and large (CL > 220 mm) female turtles during the peak of the breeding season (April–May) and the influence of three individual fixed effects: manipulation (manipulated or not manipulated in the previous year; Manip); year of capture (Yr), and the probability of surviving from 1 year to the next (Survival: high $\phi > 0.75$; low $\phi \leq 0.75$). The multi-term model Manip + Survival was also considered. Similarly, a mixed-effects model with a Gaussian error structure and an identity link function was used to test the relationship between female post-maturity growth (CL > 220 mm) and manipulation. CL was modeled as covariate (size) in all growth models. We used variance components analysis to assess the importance of the random effect site (Crawley 2007). Key life history traits can vary between populations due to site-specific differences that are not modeled as fixed effects (Fordham et al. 2007)—a situation for which Pinheiro and Bates (2000) recommend that generalized mixed effects models should not be simplified to generalized leased squares models. The goodness of fit of models to the data was tested following methods outlined by Crawley (2007). We used the multi-model inference approach advocated by Burnham and Anderson (2002) to interpret statistical models; Akaike's information criterion corrected for small sample sizes (AIC$_c$) was used to rank the models, and calculate the relative weights of evidence for each (w_i). Weighted model averaged coefficients and SEs were calculated using all models with $w_i > 0.10$, after re-scaling so that the total weights for those models that contained any given fixed effect summed to 1 (Lehmann et al. 2008). All generalized linear mixed effects models were fitted using the lmer function of the lme4 package in the R statistical package (R Development Core Team 2005).

Results

Survival

Density reduction had little influence on *C. rugosa* survival. The most parsimonious live-recaptures-only model at all three reduction sites (Imimbar, Ginmilly and Garromgarrom), related ϕ and p to turtle size (Table 1; see S3 for entire model set). Adding density reduction as a factor at Imimbar resulted in a slightly lower model ranking. There was no support for a model that related ϕ and p to reduction alone (Table 1). There was little support for modeling density reduction as an additive or sole reduction term at Ginmilly or Garromgarrom (Table 1). Model-averaged turtle survival probabilities were high prior to and after manipulation (2003–2006) at Imimbar ($\phi = 0.84$; 95% CI = 0.59–0.95),

Ginmilly ($\phi = 0.93$; CI = 0.70–0.98) and Garromgarrom ($\phi = 0.86$; CI = 0.59–0.95).

Density supplementation had little influence on *C. rugosa* survival. According to the most parsimonious combined live captures and dead recoveries model for Giddadella, severity of pig rooting had the largest influence on ϕ and p, while the recovery rate of dead animals (r) was influenced by the presence or absence of water and turtle size (Table 1; see Fordham et al. 2007 for parameter descriptions and model interpretation). Adding density supplementation as a factor at Giddadella resulted in a lower model ranking, but not substantially so. There was little support for a model that related ϕ and p to supplementation alone. The best supported survival model for the second supplementation site, Damdam, related ϕ, p and r to the presence or absence of water, while turtle size positively influenced r (Table 1). Models that treated supplementation as an additive factor in a multi-term model, or as a single-factor model, performed substantially worse. Model-averaged survival probabilities declined 8–10 months after supplementation at Giddadella ($\phi = 0.69$, CI = 0.54–0.80; $\phi = 0.47$, CI = 0.23–0.73) and Damdam ($\phi = 0.87$, CI = 0.25–0.99; $\phi = 0.39$, CI = 0.19–0.64), in response to predation by pigs, causing a substantial decline in the number of supplement animals [65% (number of fatalities = 63; CI = 21–75) and 77% ($n = 113$; CI = 65–125) decline, respectively].

Recruitment

Population growth (change in total population size) responded positively to a substantial reduction in turtle density (TD) (>50%) at Imimbar (number of turtles = 101, CI = 59–165; $n = 174$, CI = 128–272), Ginmilly ($n = 19$, CI = 4–47; $n = 58$, CI = 41–98) and Garromgarrom ($n = 15$, CI = 7–26; $n = 38$, CI = 30–49: S1). Increased juvenile numbers (CL < 140 mm) at all reduction sites in 2006 (14–17 months post-manipulation; Table 2) was characterized by a marked increase in the proportion of yearlings (Fig. 1), suggesting that a negative perturbation in turtle abundance is quickly compensated by increased hatchling recruitment (S4).

Juvenile abundance did not show a negative response to supplementation (>50% increase in density), which is surprising given the strong positive response to density reduction (Table 2). Population abundance at Damdam declined following supplementation (number of turtles = 326, CI = 262–551; $n = 220$, CI = 151–488; S1) but juvenile numbers remained relatively unchanged (Table 2). This signified that the decline in abundance was not a symptom of reduced juvenile recruitment. The number of juveniles at Giddadella increased substantially following supplementation, owing heavily to a proportional increase in hatchling

Table 1 Summary set of mark-recapture models for density reduction and supplement populations of the snake-necked turtle (*Chelodina rugosa*), showing change in Akaike's information criterion (AIC$_c$) for single-term and multi-term manipulation models with respect to the best-ranked model (Δ_i), model weights (w_i) and number of parameters (k)

Site	Treatment	Model	Δ_i	w_i	k
Imimbar	Reduced	$\phi(s)p(s^+t)$	0.00	0.50	5
		$\phi(s^+\text{red})p(s^+\text{red}^+t)$	1.79	0.21	7
		$\phi(\text{red})p(\text{red}^+t)$	10.38	0.00	5
Ginmilly	Reduced	$\phi(s)p(s^+t)$	0.00	0.68	5
		$\phi(s^+\text{red})p(s^+\text{red}^+t)$	3.94	0.09	7
		$\phi(\text{red})p(\text{red}^+t)$	11.76	0.00	5
Garromgarrom	Reduced	$\phi(s)p(s^+t)$	0.00	0.42	5
		$\phi(s^+\text{red})p(s^+\text{red}^+t)$	4.71	0.04	7
		$\phi(\text{red})p(\text{red}^+t)$	6.39	0.02	5
Giddadella	Supplement	$\phi(rt)p(rt^+t)r(\text{wrt}^+s)f(1)$	0.00	0.37	9
		$\phi(rt^+\text{sup})p(rt^+\text{sup}^+t)r(\text{wrt}^+s)f(1)$	1.17	0.21	11
		$\phi(\text{sup})p(\text{sup}^+t)r(\text{wrt}^+s)f(1)$	7.76	0.01	9
Damdam	Supplement	$\phi(\text{wrt})p(\text{wrt})r(\text{wrt}^+s)f(1)$	0.00	0.37	8
		$\phi(\text{wrt}^+\text{sup})p(\text{wrt}^+\text{sup})r(\text{wrt}^+s)f(1)$	3.29	0.07	10
		$\phi(\text{sup})p(\text{sup})r(\text{wrt}^+s)f(1)$	4.33	0.04	8

See S3 for the complete model set

Live-recapture-only models were used to model survival (ϕ) and recapture probabilities (p) at reduced treatments; combined live-recapture and dead-recovery models were used to model ϕ, p and recovery rates (r) at supplemented populations (see main text). Turtle size (*s*) was modeled as a covariate. Density reduction (*red*) and supplementation (*sup*) were treated as cofactors, as were the presence or absence of water (*wtr*) and severity of pig rooting (*rt*). Where necessary, a relative index of trapping period (*t*) averaged across all individuals in the population was modeled as an across-population covariate; $^+$ indicates additive parameters. Model parameters are described in detail elsewhere (Fordham et al. 2007)

recruits (Fig. 1; S4), causing a concomitant boost to population abundance (Table 2).

TD at the experimental control, Murrybulljuluk, did not vary significantly between 2003 and 2006 (Table 2). TD responded positively to a disturbance in 2003, which apparently displaced it from its equilibrium abundance [TD (*n*/ha) prior to disturbance = 2.4, CI = 1.6–5.3; TD immediately after a rare disturbance in 2003 = 1.8, CI = 1.3–3.5; S1], and thereby invoked a density-dependent increase in hatchling recruitment in 2004 (Fig. 1; S4) and a concomitant increase in juvenile numbers (Table 2). Similarly, TD at Little-Giddadella (unconstrained treatment) did not vary between 2003 and 2006 (Table 2). Juveniles were absent in 2003, rare in 2004, but increased in number in 2006, owing to increased hatchling recruitment (Fig. 1), responding to a negative perturbation in density in 2005 (TD prior to disturbance = 8.0, CI = 6.7–9.9; TD immediately after a rare disturbance in 2005 = 6.1, CI = 5.1–7.5; S1).

The relative weightings of the alternative generalized mixed-effects models suggest that manipulation and survival together influence hatchling abundance (2003–2006): manipulation explained the greatest amount of variance in yearling abundance (Table 3; see S5 for entire model set). The most parsimonious model had the total proportion of hatchlings as a function of manipulation and probability of survival from 1 year to the next (Hatchlings = Manip$^+$Survival; w_i = 0.809). There was less support for the saturated model (Δ_i = 2.94; w_i = 0.186) and essentially no support for any of the other models ($w_i < 0.05$). Yearling abundance was influenced by manipulation (w_i = 0.721). There was less support for the next ranked model: the two-term model (Δ_i = 2.42; w_i = 0.215). There was little support for the saturated model (Δ_i = 5.23; w_i = 0.053) and all other models ($w_i < 0.05$). Table 4 provides weighted model averaged coefficients (and SEs) for hatchlings and yearlings.

Maturity and reproduction

A downward shift in density failed to positively influence the proportion of small, reproductively active females (CL = 180–200 mm; see S6). Small female turtles were rarely gravid during the peak of the breeding season at Imimbar prior to and after reduction [20% (*n* = 5) and 14% (*n* = 7); compared to 28% (*n* = 7)]. At Ginmilly and Garromgarrom, all turtles with CLs <220 mm (*n* = 12 and *n* = 8) were not gravid, regardless of density. In contrast, large female turtles (CL ≥ 220 mm) tended to be gravid prior to and after density reduction at Imimbar [52% (*n* = 27) and 55% (*n* = 20); compared to 69% (*n* = 16)], Ginmilly [77% (*n* = 13) and 75% (*n* = 12); 83% (*n* = 18)] and Garromgarrom [78% (*n* = 9) and 75% (*n* = 8); 88% (*n* = 7)]. Moreover, increasing density did not cause a decline in the proportion of small reproductively active turtles at Giddadella. Female turtles (CL = 180–200 mm)

Table 2 Total turtle density (*TD*), juvenile population size [carapace length (CL) <140 mm], juvenile density and female annual post-maturity growth (CL > 220 mm) at manipulated and control populations, prior to manipulation (2003 and 2004), and 14–17 months after manipulation (2006)

Population	Treatment	Year	Total TD (*n*/ha)	Juvenile population size	Juvenile density (*n*/ha)	Mature female growth (mm)
Imimbar	Reduced	2003	13.4 (9.4–22.2)	8 (6–13)	0.3 (0.2–0.5)	0.4 (0.2–0.8)
		2004	10.4 (8.6–13.2)	7 (6–9)	0.3 (0.3–0.4)	0.2 (0.1–0.4)
		2006	8.1 (6.0–12.7)	44 (32–68)	2.1 (1.5–3.2)	0.8 (0.2–1.4)
Ginmilly	Reduced	2003	3.6 (2.6–5.7)	0	0	1.4 (0.7–2.2)
		2004	4.4 (3.3–6.5)	0	0	0.7 (0.2–1.3)
		2006	4.9 (3.4–8.2)	17 (12–29)	1.4 (1.0–2.4)	1.3 (0.4–2.3)
Garromgarrom	Reduced	2003	4.3 (3.5–5.6)	7 (5–9)	0.7 (0.5–0.9)	0.7 (0.2–1.4)
		2004	4.5 (3.6–5.7)	8 (7–11)	0.9 (0.8–1.2)	0.7 (0.2–1.2)
		2006	4.4 (3.5–5.7)	15 (12–20)	1.8 (1.4–2.3)	0.4 (0.0–1.3)
Damdam	Supplemented	2003	2.7 (1.8–6.2)	29 (19–65)	0.5 (0.3–1.1)	9.3 (8.0–10.7)
		2004	2.5 (1.6–5.3)	24 (16–51)	0.4 (0.3–0.9)	10.7 (9.1–13.0)
		2006	3.6 (2.5–8.0)	37 (23–89)	0.61 (0.4–1.5)	2.3 (0.9–4.0)
Giddadella	Supplemented	2003	4.9 (3.5–7.95)	41 (30–67)	1.2 (0.9–2.0)	5.7 (4.6–7.0)
		2004	3.9 (3.0–5.3)	50 (40–68)	1.6 (1.3–2.1)	5.2 (3.7–7.0)
		2006	7.9 (5.4–16.3)	141 (91–308)	3.4 (2.2–7.5)	2.9 (0.8–4.7)
Murrybulljuluk	Control	2003	2.4 (1.6–5.3)	14 (9–27)	0.2 (0.1–0.4)	1.7 (1.1–2.4)
		2004	2.6 (1.7–5.0)	62 (42–119)	0.9 (0.6–1.7)	2.3 (1.0–3.6)
		2006	3.1 (2.0–7.1)	9 (6–20)	0.2 (0.1–0.3)	2.7 (1.4–4.0)
Little-Giddaddella	Unconstrained treatment	2003	8.9 (7.6–11.0)	0	0	1.3 (1.2–1.5)
		2004	8.3 (7.2–10.3)	2 (1–2)	0.5 (0.3–0.5)	1.4 (0.4–2.6)
		2006	8.8 (7.5–10.8)	7 (6–8)	1.8 (1.5–2.0)	1.6 (0.2–3.3)

Numbers *in parentheses* are 95% confidence intervals

Turtle population size was calculated using the Horvitz–Thompson estimator (see Materials and methods)

tended to be gravid prior to and after supplementation [57% (*n* = 7) and 63% (*n* = 8); compared to 80% (*n* = 5)]. The reproductive activity of large [62% (*n* = 13) and 64% (*n* = 14); 33% (*n* = 6)] as well as small [80% (*n* = 5) and 67% (*n* = 6); 17% (*n* = 6)] females declined after supplementation at Damdam (S6).

The ranked weights of the alternative mixed effects models indicated that proportion of small, reproductively active females was not strongly influenced by survival probability, manipulation or year (S5). The most parsimonious model was Reproduction = Survival (w_i = 0.385). There was equal support for the null (i.e., a single mean rate for all individuals) model (Δ_i = 0.98; w_i = 0.236) and the model Reproduction = Yr (Δ_i = 1.67; w_i = 0.167). Similarly, reproductive activity amongst large females (CL > 220 mm) was not influenced by any of the factors modeled (S5). The null was the most parsimonious model (w_i = 0.510).
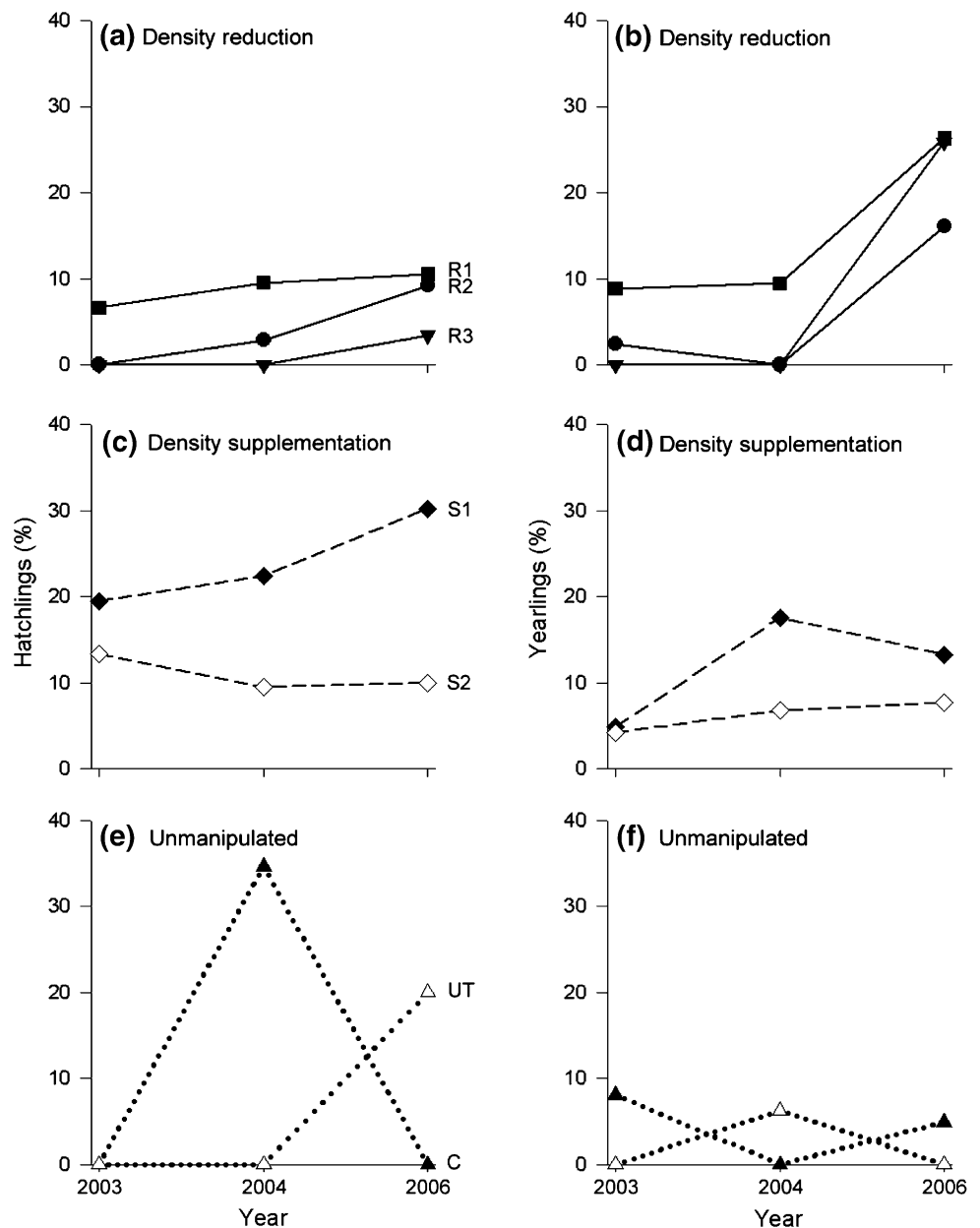
Female post-maturity growth

Annual somatic growth of large females (CL > 220 mm) was unaffected by population reduction at Imimbar, Ginmilly and Garromgarrom (Table 2). Mean growth declined significantly in response to supplementation at Damdam [9.3 mm year^{-1} (CI = 8.0–10.7) and 10.1 mm year^{-1} (CI = 9.1–13.0); compared to 2.3 mm year^{-1} (CI = 0.9–4.0)]. Mean growth declined with supplementation at Giddadella but the response was not pronounced [5.7 mm year^{-1} (CI = 4.6–7.0) and 5.2 mm year^{-1} (CI = 3.7–7.0); 2.9 mm year^{-1} (CI = 0.8–4.7)]. Growth remained relatively constant at Murrybulljuluk (control) and Little-Giddadella (unconstrained) over the same period (Table 2).

The mixed-effects models confirmed that neither manipulation, year nor annual survival strongly explained the observed variation in post-maturity growth (S5). The most parsimonious model was Growth = Size + Yr (w_i = 0.468). The model Growth = Size + Manip was ranked lower, but not substantially so (Δ_i = 1.24; w_i = 0.256). There was less support for the saturated model (Δ_i = 2.17; w_i = 0.161) and the model Growth = Size$^+$Manip$^+$Surv (Δ_i = 3.02; w_i = 0.105). There was essentially no support for any other models (w_i < 0.001). The total amount of deviance explained by each of the top ranking models was low (deviance < 5%).

Fig. 1 Percentage of total snake-necked turtle (*Chelodina rugosa*) population size represented by **a**, **c**, **e** hatchlings and **b**, **d**, **f** yearlings in 2003, 2004 and 2006, 14–17 months subsequent to population manipulation, at seven sites in northern Australia. The experimental treatments were **a**, **b** density reduction at Garromgarrom (*R1*), Imimbar (*R2*) and Ginmilly (*R3*); **c**, **d** supplementation at Giddadella (*S1*) and Damdam (*S2*); **e**, **f** an unmanipulated control at Murrybulljuluk (*C*) and an unconstrained treatment at Little-Giddadella (*UT*); see Materials and methods

Discussion

The prevailing view is that freshwater turtles do not display density-dependent responses and so harvesting sub-adult and adult turtles at almost any level is inherently unsustainable and therefore unacceptable (Congdon et al. 1993, 1994; Cunnington and Brooks 1996; Heppell 1998). This generality conflicts with the qualitative observation that freshwater turtles have been heavily exploited for human consumption for many decades (Gibbons et al. 2000) and, in the case of indigenous harvests, for many centuries. For example, *Chelodina rugosa* "harvest" populations have persisted over a long period of frequent subsistence exploitation in tropical northern Australia (Fordham et al. 2008); today introduced

pigs provide an unrelenting predation pressure on *C. rugosa*, compromising subsistence harvest rates (Fordham et al. 2006b). Through spatially replicated manipulation of population density, our new quantitative results, viewed with previous experimental and correlative research (Fordham et al. 2007; Kennett 1994), demonstrate that it is hatchling recruitment, and their survival into larger size classes, which acts to provide resilience to negative perturbations in adult and sub-adult abundance. Our results suggest that density-dependent compensation is at least partially responsible for population persistence in *C. rugosa* over the long period of interaction with people and more recently pigs.

Population growth (change in total population size) in *C. rugosa* responds positively to density reduction mainly

Table 3 Summary set of generalized linear mixed-effects models for hatchling and yearling abundance

Response	Model	LogL	k	Δ_i	w_i	Dev (%)
Hatchling abundance	Manip⁺Surv	−123.234	4	0.00	0.809	22.76
	Manip⁺Surv⁺Yr	−123.187	5	2.94	0.186	22.79
	Surv	−129.565	3	9.89	0.006	18.79
Yearling abundance	Manip	−72.292	3	0.00	0.721	21.66
	Manip⁺Surv	−72.116	4	2.42	0.215	21.85
	Manip⁺Surv⁺Yr	−72.000	5	5.23	0.053	21.98
	Yr	−76.456	3	8.33	0.011	17.15

Log likelihood (*LogL*), number of parameters (*k*), change in AIC compared to the best-ranked model (Δ_i), model weights (w_i) and percentage explained deviance (*Dev*), for the statistical relationship between hatchling and yearling abundance, and the fixed effect factors: manipulation (pre- or post-manipulation; *Manip*); year of capture (*Yr*); and the probability of surviving from 1 year to the next [high/low ($\phi \leq 0.75$ or > 0.75); *Survival*]. Note that only models with $w_i > 0.05$ are shown (see S5 for the complete model set)

Table 4 Weighted model averaged coefficients (and SEs *in parentheses*) for models describing changes in juvenile abundance

Response variable	Intercept	Manipulation	Survival
Hatchling abundance[a]	−1.73	0.60	−1.03
	(0.25)	(0.18)	(0.20)
Yearling abundance[b]	−3.24	1.02	NA
	(0.24)	(0.16)	NA

NA Non-applicable

[a] Relationship between the annual proportion of hatchlings in the population and the fixed effects, manipulation (not manipulated in previous year; manipulated in previous year) and survival (high $\phi > 0.75$; low $\phi \leq 0.75$)

[b] Relationship between the annual proportion of yearlings in the population and the fixed effect manipulation

via increased hatchling recruitment rather than compensations in survival and fecundity (Table 5), or positive density-dependent dispersal at the population level, as observed in some other vertebrates (e.g., Nichols et al. 1984; Pedersen et al. 2004). Remarkably, at some populations, TD took less than 2 years to spring back to a pre-manipulation size (Table 2; S1). Similarly, *C. rugosa* population size recovered in 1 year, following a large harvest event (which caused an estimated 22% decline in population size), owing to increased hatchling recruitment (Fordham et al. 2007). In a study on the same species from a different geographical location, juvenile recruitment responded positively to an experimental downward displacement in density (Kennett 1994).

Traits that contribute heavily to population growth in long-lived vertebrates, such as adult survival, tend to be buffered against changes in population density (Pfister 1998). Conversely, traits such as hatchling/newborn survival contribute proportionately less to population growth, but are more responsive to changes in population density (Gaillard et al. 1998). Similarly, we show that hatchling recruitment and their survival to yearlings in *C. rugosa* are more responsive to fluctuations in density than sub-adult and adult survival (Table 1). Our population manipulations coincided with the onset of the wet season, when hatchlings emerge from the nest (Fordham et al. 2006a). A large number of yearlings were recorded 14–17 months after the downward displacement in population size, indicating that density reductions were compensated swiftly by increased hatchling recruitment (Fig. 1; S4). We can be confident that the interaction between reduced TD and increased hatchling recruitment was not driven by high per capita resource availability during reproduction, because the recruits of 2005 hatched from eggs laid prior to manipulation. Instead, recovery was likely facilitated by decreased resource competition or a reduction in cannibalism. Empirical evidence from long-term and manipulative studies of fish supports this hypothesis (Rose et al. 2001).

TD remained unchanged between 2003 and 2006 in the control population at Murrybulljuluk (Table 2). TD responded positively to a disturbance in 2003 (Fordham et al. 2007), which displaced it from its equilibrium abundance (S1), causing an immediate hatchling recruitment pulse (Fig. 1; S4), resulting in a large number of 2 year olds in 2006 (Fordham 2007). Predation by pigs caused a rare periodic depression in adult survival at Little-Giddadella (unconstrained treatment) in 2005 (Fordham et al. 2007), reducing TD (S1): juvenile recruitment increased in 2006 (Table 2) owing to hatchling recruitment (Fig. 1). Correlations between reduced density and increased hatchling recruitment are consistent with earlier evidence and the a priori hypothesis that *C. rugosa* populations are regulated by density.

Population size declined following an artificial increase in density at only one of two supplemented populations. One year after supplementation, population density at Damdam declined to a density reasonably similar to that recorded prior to manipulation (Table 2). High TD at the beginning of 2005 (immediately following experimental manipulation) at Damdam negatively influenced female

Table 5 Trends in survival probabilities, juvenile abundance, proportion of small reproductively active turtles and female post-maturity growth between 2003 and 2006 at manipulated, control and unconstrained treatments. Reduced and supplemented treatments were manipulated in 2005

Population	Treatment	Response											
		Survival			Juvenile Abundance			Small Reproductive Females			Female Post Maturity Growth		
		2003	2004	2006	2003	2004	2006	2003	2004	2006	2003	2004	2006
Imimbar	*Reduced*												
Ginmilly	*Reduced*												
Garromgarrom	*Reduced*												
Damdam	*Supplement*												
Gidadella	*Supplement*												
Murrbulljuluk*	*Control*												
Little-Giddaella**	*Unconstrained*												

A rare negative perturbation in density occurred in: * 2003; ** 2005

▨ Low, uncommon or slow ▢ High, common or fast ■ Postive shift ▩ Negative shift

Note that juvenile abundance increased quickly in response to: (1) population reduction in 2005 at Imimbar, Ginmilly and Garromgarrom; (2) and a rare downward pressure on density in 2003 at Murrybulljuluk, and 2005 at Little-Gidadella. Growth rates of mature females were substantially slower at Damdam in 2006, following population supplementation

reproductive activity in 2005 and 2006 (see Results; S6), reducing the potential number of hatchling recruits. It is highly unlikely that prior resource availability suppressed reproductive activity, because *C. rugosa* annually use up the majority of their accumulated energy reserves during pre-breeding aestivation (Kennett and Christian 1994). The survival of juvenile and adult turtles was not influenced by population supplementation (Table 1); rather towards the end of 2005 (8–10 months after supplementation), pigs preyed heavily on supplemented and native turtles at Damdam (see Results) causing a strong density-independent reduction in abundance.

Population growth at Giddadella surprisingly continued to increase subsequent to supplementation (Table 2). Unlike Damdam, reproductive activity amongst native (S6) and supplemented turtles remained high, encouraging increased hatchling recruitment in 2006 (Fig. 1). TD at Giddadella at the beginning of 2005 (S1) was well below carrying capacity due to turtle predation by pigs in 2004 (Fordham et al. 2007). Resource availability prior to any given year is unlikely to influence the reproductive activity of *C. rugosa* (see above) and, as such, at a supplemented density of 6.4 turtles/ha, sufficient resources remained available at Giddadella to support an ongoing high level of reproductive activity. A rare flooding event at Giddadella in 2006 reduced TD, promoting hatchling survival and permitted a rare episode of turtle immigration (D. A. Fordham, unpublished data). In conjunction with increased number of potential hatchlings, these factors were the likely contributors to Giddadella's growth in 2006.

Small gravid turtles (CL < 200 mm) are common in *C. rugosa* populations where survival is periodically low,

yet rare in populations where survival is consistently high (Fordham et al. 2007). A shift in size of maturity towards earlier ontogenetic stages can promote persistence in response to low adult survival (Abrams and Rowe 1996). However, year–year variation in survival probability ($\phi \leq$ or > 0.75), like manipulation, does not influence the proportion of small reproductively active females (see Results). Thus, experimental evidence, viewed in conjunction with previous correlative research (Fordham et al. 2007), suggests that decreased size of maturity in *C. rugosa*, as in other reptiles (Bronikowski and Arnold 1999), and fish (Olsen et al. 2004), is probably a local adaptation—an evolved response that promotes demographic resilience under conditions of comparatively low survival.

Food availability positively influences somatic growth in long-lived vertebrates such as sea turtles (Bjorndal et al. 2000), providing an important conduit for population growth and thus resilience to density perturbations (Barlow 1992). Prior to supplementation, female post-maturity growth was rapid at Damdam and Giddadella, leading to an increase in age-specific fecundity in response to low survival (Fordham et al. 2007). Year and manipulation had some influence on post-maturity growth (S5), but the unexplained variance was large. Increasing sub-adult and adult density at Damdam induced a significant negative somatic growth response (Table 2). At Giddadella the negative growth response was not as pronounced. The determination that post-maturity growth is largely unaffected by population reduction is not unexpected, because density-dependent processes often respond nonlinearly to large fluctuations in density (Lima et al. 2002; Nicoll et al. 2003). It may be that populations of *C. rugosa* need to be held at

densities well below carrying capacity, or experience an extended period of reduced density, before a positive shift in post-maturity growth is manifested.

Perturbation analysis is difficult in tropical systems owing to multiple often highly stochastic extrinsic factors impacting on vital rates. However, quantifying population responses to density perturbations amongst tropical long-lived vertebrates is extremely important for conservation planning in tropical regions (Gaillard et al. 2000), allowing development of empirically based predictive models that forecast the impact of exploitation and other human impacts (e.g., invasive species) on species' persistence under alternative management actions (Fordham et al. 2008). Our manipulative experiments, viewed concurrently with previous experimental and correlative research (Fordham et al. 2007; Kennett 1994), are significant because they demonstrate that sub-adult and adult losses in freshwater turtles can be replaced quickly via increased hatchling recruitment and their survival into large size classes. This density-dependent response promotes resilience to high levels of harvest and predation by pigs (Fordham et al. 2008) providing: (1) a rare example of compensatory density dependence in a long-lived tropical vertebrate, and (2) the first mechanistic evidence of compensatory mortality in a turtle species.

The implications of our findings are broad, challenging the prevailing view that sustained high post-hatchling survival is crucial for achieving long-term population stability in freshwater turtles (Congdon et al. 1993, 1994; Converse et al. 2005; Cunnington and Brooks 1996; Heppell 1998). They also confirm that, like chondrichthyans (Stevens et al. 2000; Walker 1998), resilience to exploitation amongst long-lived higher vertebrates is not unequivocally low by virtue of long lifespans. We posit that the sustainability, or otherwise, of turtle harvesting should be assessed at a species level, arguing against a universal generalization that freshwater turtles are inevitably vulnerable to off-take. The harvest of turtles with "slow" life histories may warrant caution, but equally so, species with "fast" life histories, similar to *C. rugosa*, may afford a level of sub-adult and adult harvest, owing to a compensatory increase in hatchling recruitment.

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