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Feral pig predation threatens the indigenous harvest and local persistence of snake-necked turtles in northern Australia

Damien Fordham[a], Arthur Georges[a,*], Ben Corey[a], Barry W. Brook[b]

[a]Institute for Applied Ecology, University of Canberra, ACT 2601, Australia
[b]School for Environmental Research, Institute of Advanced Studies, Charles Darwin University, Darwin NT 0909, Australia

A B S T R A C T

Northern snake-necked turtles (Chelodina rugosa) traditionally provided an important seasonal source of protein for indigenous communities in Arnhem Land, northern Australia. Harvest techniques today differ little from those used historically, harvesting being applied in the late dry season when ephemeral waters have drawn down and turtles are aestivating. Radio-telemetry was used to quantify survival rates of C. rugosa at a traditional turtle harvest site and relate them to harvest, predation by feral pigs (Sus scrofa) and environmental factors. Although turtle survival was positively correlated with body size, the survival of turtles of all sizes and stages of maturity was compromised by pig predation. Seasonal variation in the onset, duration and severity of rainfall and associated influences on periodic drying, are important for C. rugosa survival because such variation influences the timing and intensity of both Aboriginal harvest and pig predation. Contemporary harvest rates of C. rugosa in Arnhem Land by Aboriginal people are very low because pig predation depletes available stocks immediately before Aboriginal harvesting. Aboriginal harvest rates are regulated also by the frequency and timing of ceremonies and other cultural activities that interfere with harvests. Before the arrival of pigs, such relaxation of harvest pressure in years when it would otherwise be possible would have contributed to the local abundance and persistence of C. rugosa. In contrast, pig predation is unrelenting, and years of high turtle survival are now restricted only to years of high wet season rainfall.

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1.   Introduction

High adult survivorship is viewed as crucial for achieving long-term population stability in turtles (Crouse et al., 1987; Heppell, 1998; Congdon et al., 2001). Mark-recapture studies demonstrate that turtles tend to have life history strategies characterised by low juvenile survivorship, delayed maturity and high adult survivorship (Brooks et al., 1991; Congdon et al., 1993, 1994). Since a small reduction in adult survivorship over time can lead to population decline in some species (Heppell and Crowder, 1996; Spencer and Thompson, 2005), human-induced changes resulting in depressed adult survivorship are of great concern (Garber and Burger, 1995; Heppell et al., 1996; Close and Seigel, 1997; Galbraith et al., 1997; Hall et al., 1999; Aiken et al., 2001; Gibbons et al., 2001). However, the life history traits and population dynamics of some turtle species may be better equipped to compensate for relatively low rates of adult survivorship than other species (Kennett, 1996, 1999; Webb et al., 2002). Reptiles that rely upon fast growth rates, a low age at onset of maturity and high fecundity can persist under conditions of relatively low adult survivorship (Fitzgerald, 1994; Shine et al., 1998, 1999).

Furthermore, some turtle species may partially compensate for decreased adult survivorship through density dependent responses (Stubbs et al., 1985; Kennett, 1994; Bjorndal et al., 2000).

The northern snake-necked turtle (*Chelodina rugosa; Chelidae*) is a fast growing, early maturing and highly fecund in comparison with other turtles (Kennett, 1994). It attains high densities in ephemeral swamps and other ephemeral wetlands of the wet-dry tropics of northern Australia. As such, it experiences the extremes of high rainfall during the monsoonal wet seasons and the near absence of rainfall in the intervening dry seasons. Turtle activity is punctuated each year by the dry season, when the wetlands "draw down" and often completely dry. Turtles survive desiccation during the dry season, typically from August/September to December/January, by burying themselves beneath the ground and aestivating (Kennett and Christian, 1994). Towards the end of the dry season aestivating *C. rugosa* provide a potential source of protein for indigenous communities living on, or near, flood plain environments (Russell-Smith et al., 1997). Women are the primary harvesters of *C. rugosa*. Rainfall in the wet-dry tropics is highly variable both within and across years in the quantity that falls and its timing (Taylor and Tulloch, 1985; Georges et al., 2003). In unusually wet years billabongs do not dry, turtles do not aestivate, and turtle harvesting is limited (Fordham, unpublished data). Accordingly, the harvest of *C. rugosa* is not necessarily an annual event.

Contemporary harvest rates of *C. rugosa* have declined at billabongs that traditionally were sites of heavy harvest (Barker, 1993). This may be a result of increasing feral pig (*Sus scrofa*), buffalo (*Bubalus bubalis*) and cattle (*Bos taurus*) densities on indigenous lands, with consequent damage to habitats, and potential direct effects of trampling on aestivating turtles and predation on nests and adults (Barker, 1993; Robinson et al., 2005). Pigs, buffalo and cattle have a devastating impact on ephemeral wetlands in northern Australia (Bowman and Panton, 1991; Mulrennan and Woodroffe, 1998). There is no evidence that declining harvest rates are the legacy of cultural transformation to meet contemporary requirements (Barker, 1993). As such, observed declines in turtle harvest returns for effort and overall yields are of a cultural concern to Aboriginal people because customary harvesting and the preparation of traditional foods are important for cultural expression, providing a vital avenue for the generational transfer of cultural knowledge (Altman et al., 1996; Freeman, 1997).

As such, distinguishing the cause of harvest decline of *C. rugosa* is of importance from a cultural as well as a management and conservation perspective. To date, the question of whether reduced harvest rates reflect a regional decline in *C. rugosa* population densities, interference with harvest methods by increased levels of feral animal disturbance at ephemeral billabongs, or a combination of these factors has not been addressed. In addressing this question, this paper assesses what factors influence aestivation in *C. rugosa* and identifies the survival cost of aestivation. Radio-telemetry was used to determine whether survivorship is continuous or punctuated by periodic drying. Focus is placed on detecting whether and to what extent turtle size, timing of aestivation, aestivation location, or aestivation depth influences survivorship. An analysis of survival in response to harvest and predation is included, allowing interpretation of the relative impact of contemporary harvest rates on *C. rugosa* populations in Arnhem Land. These findings are discussed against a backdrop of stochasticity in the timing, duration and extent of the seasonal availability of surface water.

2. Methods

2.1. Study location

The *C. rugosa* population at Gid-da-della billabong, an ephemeral billabong located in central Arnhem Land, Northern Territory (134°21′S; 12°31.55′E), was studied over a 6 year period from 2000 to 2006 as part of a broad study focused on the demographic impact of *C. rugosa* harvesting in the Maningrida region. Gid-da-della is a traditional *C. rugosa* harvest site for the Rembarranga people.

2.2. Radio-telemetry

Towards the end of June 2005, turtles were caught at Gid-da-della over a two week period using fyke net traps. Forty turtles were chosen on the basis of size and sex. Carapace length was divided into eight size classes and five turtles were chosen at random from each size class (<130 mm, 130–145 mm, 145–160 mm, 160–175 mm, 175–190 mm, 190–205 mm, 205–220 mm, >220 mm). Where possible, turtles from both sexes were proportionately represented in each size class. Turtles were removed from the billabong for a period of seven days to secure Sirtrack® customized transmitters (Sitrack; Havelock North, New Zealand). Transmitter size was matched to body size to ensure that the weight of the transmitter did not exceed 7% of turtle weight (Schubauer, 1981). Transmitters were affixed by stainless steel bolts through holes drilled in the margin of the carapace (Tucker et al., 2001). Selly's Aqua Seal Putty® was used to create a level surface between the transmitter and the shell. In accordance with published protocols, the antenna trailed behind the turtle (Boarman et al., 1998). Transmitters were attached to turtles ranging in size from 111–276 mm. This allowed us to test the possibility that size influences turtle movement, timing and location of aestivation and survivorship.

After attaching the transmitter, turtles were held for a 5–6 day monitoring period before release. Turtles were released early July and tracking commenced after 7 days and continued until mid October 2005. As such, turtles were tracked prior to, during and immediately after the draw down period at Gid-da-della. Turtles were tracked at a standard three day interval using Telonics TR-4 receivers (Telonics; Mesa, AZ) fitted with Yagi collapsible antennas (model AY/C; Titley Electronics, Ballina, NSW). GPS location (Garmin 'GPS 72'; Garmin; Olathe, Kansas), water depth (to the nearest cm), and habitat were recorded for each animal on each tracking occasion. Turtle movement was calculated using the ArcView 3.2® extension Animal Movement Analysis (Hooge and Eichenlaub, 1997). Turtle location was successfully established on all occasions during the entirety of the study for 38 of the 40 turtles. Data from the two outstanding turtles

180 were excluded from the analysis. Individual turtle movement
181 was calculated as the distance between subsequent fixes
182 according to the inter-tracking period. Average turtle move-
183 ment was calculated as the average distance of movement be-
184 tween tracking events for non-aestivating turtles.

185   Radio telemetry was used to identify aestivation sites, and
186 a probing stick (blunt 10 mm diameter steel rod) was used to
187 confirm the precise location of the aestivating turtle. Location
188 and description of the aestivation site was recorded, and four
189 250 mm steel pickets were used to construct a 1 m^2 plot
190 around the aestivating turtle. Pickets were inserted into the
191 ground to a depth of 100 mm. By minimizing picket height,
192 and by spacing pickets 1 m apart, plot access by predators
193 was not impeded. Since disturbance was monitored without
194 entering the plot, there is no reason to believe that the con-
195 struction of aestivation plots attracted predators. Every three
196 days a digital photo was taken of the plot (Nikon D100®). Pred-
197 ator type was assessed by identifying tracks and scats within
198 the plot. This procedure allowed us to identify the source and
199 timing of predation within a three day period.

200   Aestivation depth relative to pig rooting depth was tested
201 to determine whether C. rugosa avoid detection during aesti-
202 vation by virtue of aestivation depth. Once Gid-da-della dried,
203 a random selection of 100 pig roots (holes dug whilst feeding)
204 was chosen according to published methodology (Hone, 1988).
205 Mounded earth surrounding the root was removed and a steel
206 rod was placed across the width of each root. A tape measure
207 was used to measure root depth and straight-line vertical dis-
208 tance from the deepest point of the root to the steel rod.

2.3. Billabong indices

210 Decrease in water surface area, water depth, invertebrate
211 diversity and density, and increased water temperature were
212 identified a priori as possible triggers of aestivation in C. rug-
213 osa. Water temperature was monitored hourly from early
214 June–mid September using Hobo Water Temp Pro® data log-
215 gers (Onset Computer Corporation, Meadowbank, PA). Water
216 temperature was measured at the deepest point of the billa-
217 bong, at a depth of 10 cm from the bottom. Water surface
218 area, water depth and standing invertebrate crop were re-
219 corded at fortnightly intervals. Surface area was calculated
220 by circumnavigating the billabong recording location points
221 at 100 m intervals using a GPS. ArcView GIS 3.2® software
222 was used to calculate water surface area from perimeter loca-
223 tion points. Surface area was scaled, by dividing observed sur-
224 face area by maximum surface area recorded at the end of the
225 wet season. Water depth was measured at a standard location
226 with a tape measure. Standing invertebrate crop was mea-
227 sured according to published protocols (Georges et al., 1986)
228 as follows. A column sampler (cross sectional area 0.07 m^2)
229 was placed on the bottom at a water depth of 30 cm. All aqua-
230 tic vegetation was removed from the column and placed into
231 a sampling bucket. A small hand net (500 μm mesh) was
232 moved 15 times through the water contained in the column
233 and on each occasion the contents of the net were emptied
234 into the sample bucket. Five replicates from each compass
235 quarter (north, south, east and west) were taken on each sam-
236 pling occasion. A basic sort of each sample occurred in the
237 field, prior to being preserved in a 10% formalin solution. A

238 secondary sort occurred prior to identification, counting and
239 weighing. Where possible, invertebrates were identified to
240 the family level.

2.4. Pig gut analysis

242 In the last week of July and the first week of August, 30 pigs
243 were shot and dissected. The stomach, upper and lower intes-
244 tines were removed for analysis. Pigs were shot by the Bawin-
245 anga Aboriginal Corporation Djelk Rangers in conjunction
246 with the regional feral animal management plan for the
247 Maningrida region. The pigs were shot at Damdam billabong,
248 located approximately 80 km north east of Gid-da-della. Pigs
249 were targeted as the billabong began to dry and turtles pre-
250 pared for aestivation. Pigs were shot at first light whilst feed-
251 ing in the billabong. Since pigs tend to harbour in the shade
252 during the day (Bowman and McDonough, 1991), this sam-
253 pling technique provided a high probability that each pig
254 had spent at least part of the night feeding at Damdam billa-
255 bong. Pigs with a body size greater than 50 kg were sampled.
256 Males and females were sampled equally to prevent any pos-
257 sible sex bias in feeding location or food choice. Pigs were dis-
258 sected on site. The stomach and intestines were bagged and
259 transported back to laboratory facilities at Maningrida for
260 analysis. The contents of the stomach and intestines were
261 rinsed using a fine mesh sieve and spread across sorting
262 benches. A presence/absence list was compiled for each sam-
263 ple. The proportional presence of each of the main dietary
264 groups was estimated.

2.5. Harvest rates of Turtles

266 Harvest rates at Gid-da-della were assessed between 2000 and
267 2006. Where possible, data was gathered by accompanying
268 harvesters during harvest events. The straight-line carapace
269 length and sex of harvested turtles were noted. This allowed
270 us to test whether harvesters display a size/sex bias in har-
271 vesting. We were unable to accompany harvesters on all har-
272 vesting events. On these occasions, community members at
273 Kolorbidahdah (location where the majority of harvesters re-
274 side) were asked to store the shells of harvested turtles. As
275 such, our harvest estimates should be viewed as an index of
276 harvest intensity. Although the community actively saved
277 the shell of most turtles harvested from Gid-da-della, some
278 turtles were sent to family members residing outside of Kolor-
279 bidahdah while dogs scavenged the shells of some other tur-
280 tles. No attempt was made to include an estimate of shell loss
281 in our harvest data and hence our harvest estimates rates dis-
282 play a degree of downward bias.

2.6. Statistical analysis

284 The known fate extension of Program Mark 4.2 (Colorado
285 State University; White and Burnham, 1999) was used to esti-
286 mate survivorship during aestivation at Gid-da-della. The R
287 statistical package v2.1.1 (R Development Core Team, 2005)
288 was used for analysis external to Mark. Known fate models
289 are the preferred method for testing survivorship using radio
290 telemetry data (Heisey and Fuller, 1985; White and Garrot,
291 1990). Two turtles were eliminated from the data set because

292 they did not meet the assumptions of the model; their fate
293 could not be confirmed. A set of candidate models developed
294 *a priori* was formulated in Mark and Akaike Information Crite-
295 rion (AIC$_c$) corrected for small sample size was used as an
296 objective means of model selection. The AIC$_c$ chooses the
297 most parsimonious model from a candidate set of models.
298 This is the model with greatest support from the data (i.e.
299 closest Kullback–Leibler distance to an unknown "truth";
300 Burnham and Anderson, 2001), given the bias corrected max-
301 imized log-likelihood of the fitted model and a penalty for the
302 number of parameters used. Turtle size and days to aestiva-
303 tion were modelled as individual covariates. Average turtle
304 movement of non-aestivating turtles and water surface area
305 were averaged across all individuals in the population and
306 modelled as across population covariates. The presence/ab-
307 sence of water was treated as a co-factor.

2.7. Taxonomic clarification

309 Throughout this paper, our study species is referred to as the
310 Northern Snake-necked Turtle *Chelodina rugosa* (Ogilby, 1890).
311 There is some confusion on this designation because the
312 holotype of *C. oblonga* (Gray, 1841) is a specimen of our study
313 species (Thomson, 2000). The name *C. oblonga* takes prece-
314 dence. Strictly then, our study species is *C. oblonga*, a name
315 that was applied to it up until 1967. Since then, it has been
316 consistently but erroneously referred to as *C. rugosa*. However,
317 an application is before the International Commission for
318 Zoological Nomenclature (ICZN) to conserve current usage
319 of the name *C. rugosa* Ogilby, 1890 for the Northern Snake-
320 necked Turtle (Thomson, 2006). In the interests of stability
321 of nomenclature, and because this application is under con-
322 sideration by the ICZN, *C. rugosa* is used as the name of our
323 study species.

3. Results

3.1. Location and timing of aestivation

326 Turtles generally aestivated amongst clumps or under fallen
327 mats of the sedge *Eleocharis dulcis* (90%) rather than amongst
328 the roots of paperbark trees *Melaleuca leucadendra* (10%). Aes-
329 tivation in *C. rugosa* did not occur at a specific, well defined
330 point in time but rather turtles cumulatively entered aestiva-
331 tion over a 30 day period. Average turtle movement declined
332 sharply prior to this period (Fig. 1). Turtles entering into aesti-
333 vation moved to the shallows (water depth <12 cm) and par-
334 tially buried themselves in the mud, digging deeper as the
335 water receded. Once partially buried in the wet mud, turtles
336 tended only to move in response to disturbance. Timing of
337 aestivation was influenced by size, smaller turtles tending
338 to aestivate earlier. Based on the evidence ratio (ER), the linear
339 model was 22.31 times better supported by the data
340 ([w[size] = 0.957]/[w[null] = 0.043] = 22.31). However, aestiva-
341 tion location (distance from aestivation site to the deepest
342 point of the billabong) was independent of size. The null
343 (intercept) model was 2.62 times better supported by the data.
344   Water surface area and water depth declined prior to and
345 during the final draw down period, while water temperature
346 increased during this period (Fig. 1). Invertebrate biomass in-
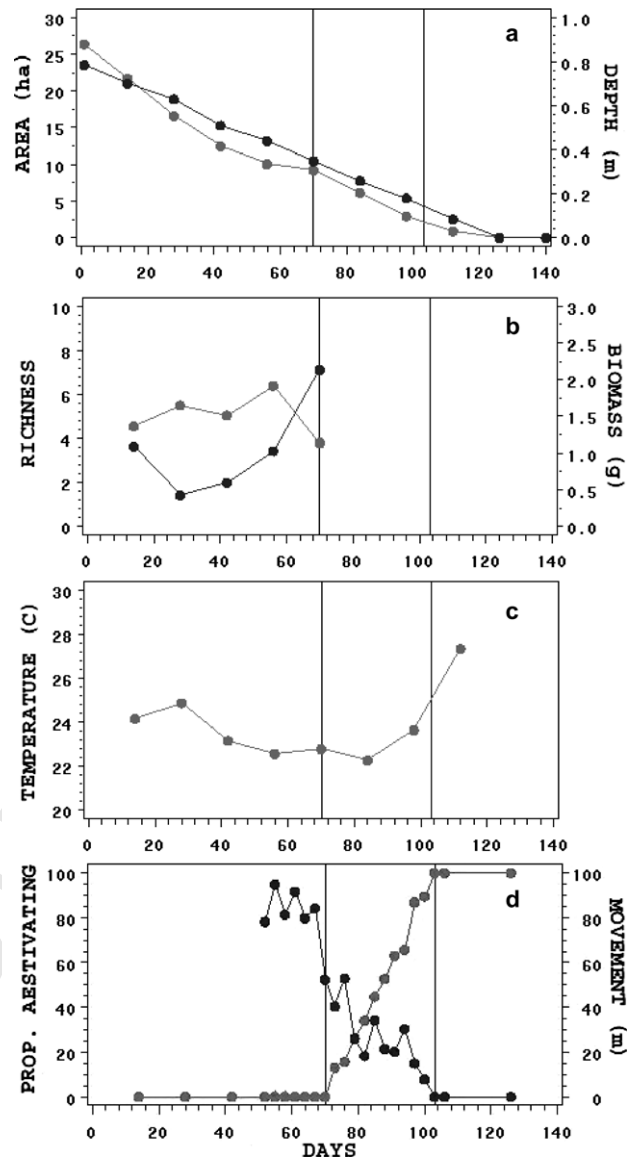
Fig. 1 – The drawdown period at Gid-da-della is characterised by a linear decline in water surface area and water depth. Vertical bars characterise the window of opportunity available for initiating aestivation (a). Invertebrate biomass increased, while invertebrate diversity decreased prior to the final draw down period (b). Water temperature rose during this period (c). Turtles slowed their movement and entered into aestivation over a 30 day period (d). Cumulative count of aestivating turtles depicts aestivation as a gradual process, responding to one or a combination of factors such as a declining water area, declining water depth, declining invertebrate diversity and increasing water temperature. Note: the x-axis documents days from first monitoring period, not inter-aestivation period, see methodology.

347 creased immediately prior to the final drawdown period,
348 while invertebrate diversity declined. The observed increase
349 in invertebrate biomass prior to the final draw down phase
350 was the result of a high representation of singular species
351 of backswimmer, family Notonectidae (Order: Hemiptera).

352 The correlates tested failed to identify a single obvious cue for
353 aestivation in *C. rugosa*.

3.2. Pig predation

355 The fates of 38 of the 40 tracked turtles were successfully
356 determined prior to, during and immediately after the final
357 draw down period at Gid-da-della. The tracking history of
358 the outstanding two animals was eliminated from the analy-
359 sis since neither transmitter failure nor migration could be
360 discounted. Of these 38 turtles, only 10 turtles (26%) were
361 alive at the completion of tracking (Fig. 2). Survival of unsexed
362 juveniles ($n = 5$), males ($n = 16$) and females ($n = 17$) was low.
363 Only 20% of juveniles, 19% of males and 35% of females were
364 alive at the completion of the study. Furthermore, only 36% of
365 turtles with carapace lengths equal to, or greater than,
366 165 mm (adult male and sub-adult and adult female turtles;
367 Kennett, 1994) survived. Pigs were the main predator. Re-
368 corded tracks and disturbance in aestivation plots indicate
369 that pigs were the cause of 27 of 28 recorded deaths (96%).
370 White Ibis (*Threskiornis molucca*) was identified as the only
371 other predator of *C. rugosa*.
372 Pig dietary analysis confirmed that male and female pigs
373 prey on *C. rugosa*. Shell fragments were found in the stomach
374 and or large intestines of 16 of the 30 pigs sampled (53%) and
375 of these 16 animals, 10 were male (62.5%) and 6 were female
376 (37.5%). Vegetative bulbs and rhizomes of *E. dulcis* and *E.
377 sphacelate* constituted the majority of each sample. Inverte-
378 brates, in particular red claw yabbies (*Cherax quadricarinatus*),
379 were common. An estimate that 53% of pigs consumed turtle
380 during the previous evening should be viewed as a minimum
381 estimate because of the difficulty in identifying fragments of
382 crushed turtle shell in pig dietary samples. Pigs do not tend to
383 eat the shells of larger turtles and turtles consumed at the
384 beginning of the evening may have past through the digestive
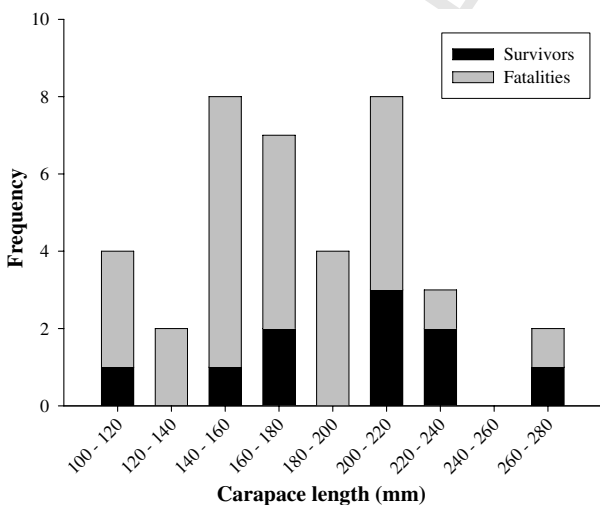385 system prior to sampling in the morning.

Fig. 2 – Survival of turtles tracked during the draw down period at Gid-da-della. Note that a large proportion of adult male and sub-adult and adult female turtles (carapace lengths equal to, or greater than 165 mm) died.
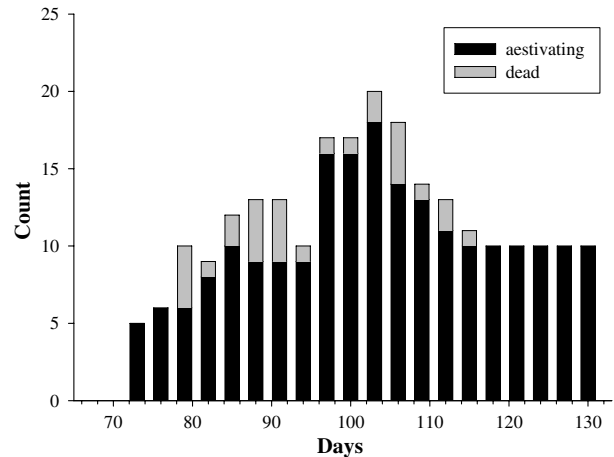

Fig. 3 – Predation of aestivating turtles during the draw down period at Gid-ad-della. Note that turtle predation began shortly after turtles commenced aestivating (after 73 days of monitoring at Gid-da-della). Also note that predation ceased when the billabong dried (after 118 days of monitoring at Gid-da-della). Ten turtles were alive at the conclusion of the study.

386 Pigs provide a steady predation pressure on *C. rugosa* dur-
387 ing the final draw down period. Predation is alleviated only
388 when the billabong dries and pigs disperse to the surrounding
389 savannah (Fig. 3). Photos of aestivation plots over time re-
390 vealed that pigs target aestivating turtles. In 11 out of the 27
391 cases of pig predation (41%), pigs specifically located and
392 dug up the aestivating turtle, leaving the remainder of the
393 1 m^2 plot undisturbed. This indicates that pigs actively seek
394 out and prey on aestivating turtles. Shells of turtles with car-
395 apace lengths less than 160 mm tended to be heavily crushed
396 during pig predation, the majority of the shell being con-
397 sumed. In contrast, pigs favour the extremities (neck, leg
398 and head) of larger turtles, leaving the shell damaged and
399 only partially consumed. Aestivation depth did not exceed
400 rooting depth and therefore did not assist *C. rugosa* survivor-
401 ship. Average depth of aestivation was 11 cm ($n = 10$), while
402 average rooting depth was 19.04 cm ($n = 100$). Aestivation
403 depth was not influenced by body size. The null model was
404 6.8 times better supported by the data.

3.3. Aboriginal harvest

406 Aboriginal harvest rates were extremely low at Gid-da-della.
407 Harvests were attempted at the billabong in 2002 ($n = 13$),
408 2003 ($n = 10$), 2004 ($n = 8$) and 2005 ($n = 0$). Note that no turtles
409 were captured during harvest events in 2005. The harvest re-
410 gime focused on turtles with carapace lengths greater than
411 150 mm (Fig. 4). As such, sub-adult and adult turtles were
412 the harvested cohorts.

3.4. Survivorship analysis

414 The most parsimonious survival model for *C. rugosa* at Gid-
415 da-della over the study period was $\phi(m^+s^+w)$ (AIC$_c$ $w = 0.8214$
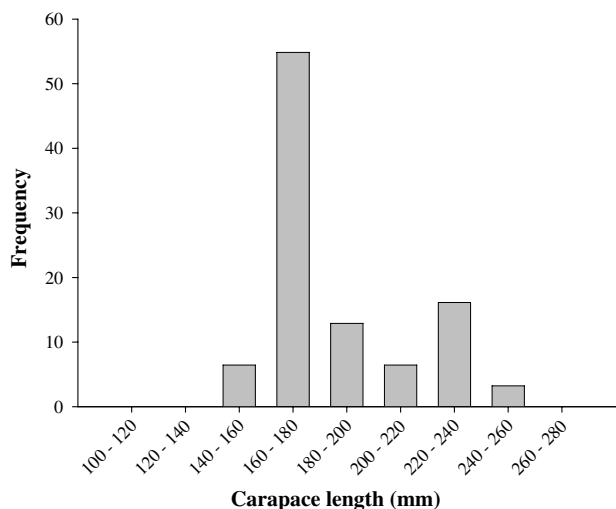416 out of a sum of 1.0); that is, survival (ϕ) was dependent on

Fig. 4 – Turtles harvested at Gid-da-della from 2000 to 2005. Note that harvesting focused on turtles with a carapace length greater than 150 mm (adult and sub-adult turtles).
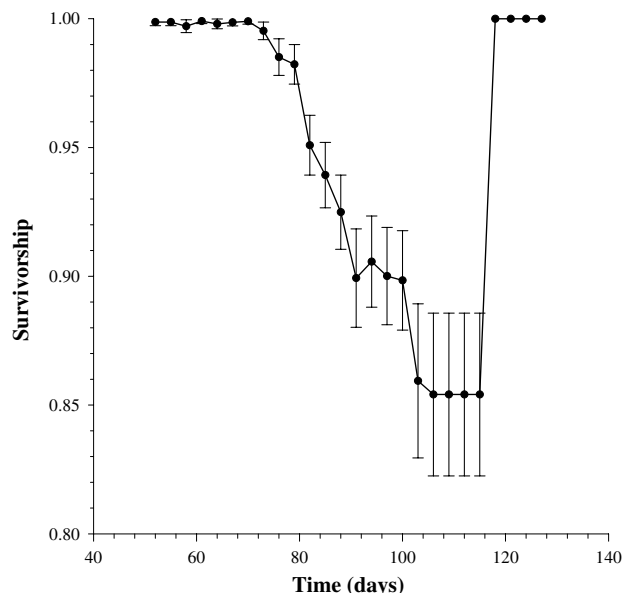

Fig. 5 – Survivorship at Gid-da-della according to the most parsimonious model $\phi(s^+m^+w)$. Note that survivorship levels begin to drop once turtles start to enter into aestivation (after 73 days) remaining relatively low until the billabong dries (after 118 days).

average turtle movement between tracking events, size, and the presence or absence of water at the billabong. A size-independent variant of this model $\phi(m^+w)$ received considerably less support from the data ($\Delta AIC_c = 4$; $AIC_c w = 0.111$) as did the model $\phi(m^+s^+a)$ (Δ $AIC_c = 5.45$; $AIC_c w = 0.0539$), where water presence/absence was substituted with a measure of water surface area over time. All other candidate models lacked any support from the data (Table 1). Note that the coefficients of the most parsimonious model ($\phi(m^+s^+w)$) show that survival, although being positively influenced by size, decreases as turtles begin aestivating, returning to pre-aestivation levels once the billabong dried (Fig. 5). Since decline in average turtle movement is a good proxy for initial aestivation (Fig. 1), the importance of movement as a factor in the survivorship model demonstrates that early aestivation is a time of predator vulnerability. Survivorship of turtles over the tracking period of 81 days was $\phi = 0.2371$ (standard error = 0.0687) with upper and lower 95% confidence intervals of $\phi = 0.1286$ and $\phi = 0.3955$ respectively.

4.   Discussion

Our radio-tracking monitoring demonstrates a number of remarkable results. First, survivorship in *C. rugosa* is greatly reduced during the end of the dry season when wetlands draw down and turtles aestivate. Only 26% of study animals tracked during the draw down period at Gid-da-della survived. Second, adult survivorship was heavily reduced during the draw down period. High adult survivorship in response to delayed maturity is often viewed as essential in achieving stability in turtle populations (Brooks et al., 1991; Congdon et al., 1993, 1994; Heppell and Crowder, 1996; Hall et al., 1999). Turtles grow rapidly in size until maturity (a carapace length of 165 mm for male and 210 mm for female *C. rugosa*; Kennett, 1994), maturing at a minimum size where survivorship re-

Table 1 – Complete survivorship model set showing Akaike's Information Criterion (AICc), number of parameters, deviance, and model weights

Model	AICc	Parameters	Deviance	Delta AICc	Weight
$\phi(m^+s^+w)$	186.733	4	180.698	0	0.828
$\phi(m^+w)$	190.736	3	186.719	4	0.112
$\phi(m^+s^+a)$	192.183	4	184.124	5.45	0.054
$\phi(m^+s)$	196.847	3	190.812	10.11	0.005
$\phi(m)$	200.84	2	196.822	14.11	0.001
$\phi(a)$	216.017	2	211.999	29.28	0
$\phi(w)$	228.492	2	224.474	41.76	0
$\phi(s)$	229.615	2	225.598	42.88	0
$\phi(\cdot)$	229.782	1	227.776	43.05	0
$\phi(da)$	231.773	2	227.756	45.04	0

Model names reflect parameters used in the model. Turtle size (s), days to aestivation (da), average movement between tracking events (m) and water surface area (a) were modelled as covariates. Water presence/absence (w) was treated as a co-factor (refer to methods). The time constant model ($\cdot$) was also modelled.

mains high (Congdon and Gibbons, 1990; Gibbons and Lovich, 1990). Our results indicate that post-maturity size does not guarantee high survivorship in *C. rugosa*. Only 36% of turtles tracked with carapace lengths of 165 mm or greater survived the initial aestivation period. Third, the impact Aboriginal harvest rates have on *C. rugosa* survivorship is negligible compared to predation by feral pigs. Poor harvest success at Gid-da-della (traditionally a site of high harvest for Rembarranga people) appears to be the direct result of harvesters competing with pigs for a seasonal food source.

Aestivation in *C. rugosa* does not occur at a specific, well defined point in time, but rather over the weeks prior to the billabong drying. Turtles move to the shallows and partially bury themselves in the mud, digging deeper as the water recedes and moving only in response to disturbance. Turtles at Gid-da-della did not emerge from the billabong to aestivate in a dry substrate, as has been previously suggested for *C. rugosa* (Grigg et al., 1986). Turtles that commence aestivation in the shallows breathe by raising their head above the water surface (Kennett and Christian, 1994). In turn, breathing constrains turtles from initially burying themselves deep in the mud. Aestivation in *C. rugosa* is probably an adaptive response to a number of interacting factors during the final draw down period, such as declining water availability, increased water temperature and decreased invertebrate diversity (Fig. 1).

Survival rates recorded for *C. rugosa* at Gid-da-della are much lower than previous estimates for this species (Kennett, 1994) and for turtles in general (Frazer et al., 1991; Iverson, 1991; Congdon et al., 1993; Spencer and Thompson, 2005). We are confident that the tracking procedures used in this experiment did not bias our survivorship estimate in a downward direction. Human interaction between tracker and turtle was minimized at all times. Transmitter weight did not exceed 7% of turtle body mass and hence did not restrict turtle movement (Schubauer, 1981). Rather, low *C. rugosa* survival at Gid-da-della is a direct response to high pig abundance during the final draw down period. Feral animal numbers were relatively low and harvesting absent at previously studied populations and, in turn, *C. rugosa* survivorship was measured to be relatively high (Kennett, 1994). Survivorship of *C. rugosa* at Gid-da-della, according to the most parsimonious survivorship model $\phi(s^+m^+w)$, reveals that size positively promotes survival during the final draw down phase, when turtles commence aestivation, burying in the mud and ceasing daily movement and thus minimising daily expenditure (approximately 30 days at Gid-da-della in 2005). During this period the billabong had drawn down, but had not dried completely. Pigs concentrate around available water during the late dry season in northern Australia (Caley, 1993; Twigg et al., 2005). Accordingly, pigs dispersed from Gid-da-della when the billabong dried, causing survival rates to return to a level similar to that observed prior to the final draw down phase (Fig. 5). The challenge is to interpret these new findings in context, where aestivation is not necessarily an annual event, where rock paintings and ceremonial stories indicate that turtle populations have survived an antiquity of many millennia of harvesting (Chaloupka, 1993) and where recently invasive pigs are now in high abundance across northern Australia (Caley, 1993; Corbett, 1995).

Harvest methods used to gather *C. rugosa* today differ little from those used historically (steel rods are often substituted for wooden digging sticks) and as such the contemporary harvest regime can be viewed as a window to the past. Harvesters still use the excavation mound and the breathing hole of aestivating turtles as the primary method for locating *C. rugosa*. The data presented in this paper show that harvesting focuses on sub-adult and adult turtles (Fig. 4), the most important cohort for achieving population stability (Crouse et al., 1987; Heppell and Crowder, 1996; Heppell, 1998). *C. rugosa* grows quickly, matures at a young age and is highly fecund (Kennett, 1996, 1999). Such demographic characteristics promote population stability in environments where adult survivorship is low (Fitzgerald, 1994; Shine et al., 1996; Webb et al., 2002). Although our data suggest that contemporary harvest rates of *C. rugosa* in Arnhem Land are minimal, as recently as 10–20 years ago *C. rugosa* provided an important seasonal source of protein for Aboriginal people in Arnhem Land (Altman, 1984; White and Meehan, 1993; Russell-Smith et al., 1997). Our data suggest that the observed decline in harvest rates do not reflect over harvesting, or a cultural shift in the emphasis placed on turtle harvesting today, but rather declining harvest rates are the direct result of the timing and severity of *C. rugosa* pig predation. The harvest techniques used to gather *C. rugosa* limit harvesting to a dry environment. Since pig predation causes a substantial decline in *C. rugosa* survival rates during the weeks prior to drying, pigs deplete harvest stocks immediately before the harvest event, in turn causing harvest success to decline. Harvest rates are further compromised by pigs rooting billabongs whilst digging up the bulbs and roots of *E. dulcis*, *E. sphacelate* and *Nymphaea sp.*, making the location of aestivating turtles a difficult task.

Our research spawns an interesting question. Do pigs prey upon a proportion of the turtle population that would otherwise be doomed as a result of customary harvesting? Evidence suggests that *C. rugosa* achieve relatively high survivorship rates in the absence of high pig densities (Kennett, 1994). As such, it is logical to assume that this would in turn convert to increased harvest efficiency, especially since harvest efficiency rises when feral animals are absent or in low density during the draw down period (Fordham, unpublished data). Therefore, it is probable that harvesting would have otherwise sealed the fate of a proportion of the turtles predated by pigs at Gid-da-della. However, the potential threat pigs pose to *C. rugosa* populations in Arnhem Land is not necessarily lessened by the fact that pig predation, to an extent, replaces Aboriginal harvesting.

Persistence of *C. rugosa* in Arnhem Land historically has been influenced by a combination of stochastic rainfall and cultural practices on customary harvest rates. Although billabongs annually rise and fall in accordance with the monsoonal wet season and the intervening dry season, drawdown and billabong drying is not necessarily an annual event. Rainfall in northern Australia is subject to extreme temporal variation (Taylor and Tulloch, 1985; Georges et al., 2003), providing years where *C. rugosa* aestivate and years where aestivation is not required. In years where aestivation is not required, survivorship remains high and the compensatory mortality period is extended; these are boom years (2000 and 2001 at Gid-da-della). Conversely, in dry years billabongs

draw down, the turtles aestivate and survivorship is low; these are potentially the bust years (2002–2005 at Gid-da-del-la). However, Aboriginal people are bound by cultural responsibilities that are reinforced through participation in ceremonies and rituals (Berndt and Berndt, 1970). These cultural practices often mean that billabongs are left unharvested since ceremonies in Arnhem Land normally coincide with the late dry season when *C. rugosa* are harvested. Furthermore, traditional estates are often periodically closed for ritual purposes, meaning subsistence hunting and gathering is prohibited creating spatial refugia (Fordham, unpublished data). Before the introduction of pigs, these potential bust years would have constituted boom years for those local *C. rugosa* populations. The frequency of boom years, seasonally driven as well as by lapses in Aboriginal harvest, and matched with a favourable set of life history traits, have enabled *C. rugosa* populations in Arnhem Land to withstand a history of adult harvesting. The arrival of pigs, with their unrelenting attention to turtle predation, has changed this dynamic. The high rainfall boom years for turtle survivorship, no longer complemented by years in which Aboriginal harvest is interrupted by cultural activity, are now likely to be much more important in determining adult survivorship and the stability of populations of *C. rugosa* in Arnhem Land than before pigs arrived.

A comparison of pig predation on *C. rugosa* with fox (*Vulpes vulpes*) predation on the Murray turtle (*Emydura maquarii*) illustrates the importance of boom years and favourable life history traits to the persistence of *C. rugosa* in Arnhem Land. Foxes, an animal exotic to Australia, prey on nesting *E. maquarii* (Thompson, 1983; Spencer, 2002). Although survivorship rates of *E. maquarii* are relatively high compared to those recorded for *C. rugosa* at Gid-da-della, fox predation may cause long-term population decline in *E. maquarii*, primarily because the life history traits of *E. maquarii* are ill-equipped to compensate quickly for adult predation during the interbreeding season and, in the absence of human intervention, predation is an annual event (Spencer and Thompson, 2005).

The direct conservation implications of pig predation on *C. rugosa* in Northern Australia remain uncertain. The present study shows that *C. rugosa* populations can potentially persist despite episodes of heavy pig predation if wet years are frequent, providing annual persistence of water at seasonal billabongs, since survival rates remain high in the absence of drying. The harvest and related cultural implications of pig predation are clearer. Dietary studies of Aboriginal people in central Arnhem Land indicate that pigs were locally rare or nonexistent only 30 years ago (Altman, 1984, 1987), and as such it is likely that pig populations in Arnhem Land are yet to reach carrying capacity. Since pigs are the main predator of *C. rugosa*, one can expect that *C. rugosa* survivorship will decline further with increased pig abundance and, in turn, *C. rugosa* harvest efficiency in Arnhem Land will continue to dwindle. In the near future Aboriginal people may have no choice but to abandon the harvest of *C. rugosa*, an action that will have damaging cultural consequences. The cultural reinforcements linked to harvesting and preparing traditional foods exceed dietary requirements associated with forging a subsistent lifestyle (Collins et al., 1996; Freeman, 1997). Harvesting provides an important conduit for the generational transfer of traditional knowledge and cultural history. The forced abandonment of *C. rugosa* harvesting in response to predation by feral pigs threatens to constitute yet another hardship on indigenous societies in northern Australia. Customary harvest rates are already compromised by the invasive cane toad (*Bufo marinus*; Altman et al., 2003), an exotic anuran that threatens the persistence of a number of terrestrial reptiles in northern Australia (Burnett, 1997; Phillips et al., 2003). However, pigs in Arnhem Land present a management paradox since feral animals often constitute a culturally and economically important resource for indigenous people (Altman, 1982; Bowman and Robinson, 2002). Communities at a regional level must collectively choose between an annually available food source in the form of pig meat and conserving the traditional harvest of *C. rugosa*, a food source that is at best seasonally abundant. Effective management can only be achieved if all stakeholders choose to view pigs as a pest (Robinson and Whitehead, 2003). Management issues that are a direct legacy of post colonialism, such as formerly domesticated feral animals, often rely upon the amalgamation of traditional and western scientific practices to achieve "healthy" country (Barker et al., 2001; Whitehead et al., 2003). Accordingly, it is imperative that government agencies and scientists work together with indigenous communities to outline both the potential threat pigs pose to harvest rates and possibly the persistence of *C. rugosa*, and the management options available to manage pig abundance in Arnhem Land such that *C. rugosa* harvesting can continue into the future as it has for countless generations.

Predictive demographic models that incorporate stochastic rainfall, recruitment, pig densities and any compensatory responses to predation are urgently required to assess the population dynamics and persistence probabilities of *C. rugosa* in Arnhem Land. In doing so, this research will provide further insight into the conservation threat pigs pose to *C. rugosa* populations across Northern Australia.

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