



Harvesting predators: simulation of population recovery and controlled harvest of saltwater crocodiles *Crocodylus porosus*

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6 egg harvest that should be accounted for in future harvest scenarios.

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8 **Harvesting predators: simulation of population recovery and controlled harvest of**
9 **saltwater crocodiles *Crocodylus porosus***

10

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12

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20

21 **Abstract (<350 words)**

22 *Context*; The population of saltwater crocodiles *Crocodylus porosus* in the Northern
23 Territory, Australia has been recovering from a period of intensive, unregulated harvest (1945
24 to 1971) since protection in 1971. Consequently, the management goal is shifting from
25 restoring a seriously depleted population to managing an abundant population through
26 controlled harvests for both commercial purposes and public safety. *Aims*; We conducted this
27 study to 1) examine whether the controlled harvest of eggs and adults since protection has
28 had an adverse effect on population size and structure, and 2) explore the effect of future
29 harvest scenarios on population size and structure by adjusting harvest levels of both eggs
30 and adults. *Methods*; On the basis of 40 years population monitoring data and knowledge of
31 population attributes from previous research, we developed density-dependent, structured
32 matrix population models to explore our aims. *Key results*; The models supported that the
33 depleted population recovered rapidly under protection and that the harvest rates since
34 protection were benign. The model estimated the 2017 harvested population, 46 years after

35 protection, to be approximately 102 000 non-hatchlings (>0.6 m crocodiles), of which 42.2%
36 are large (>2.1 m total length) individuals. This is similar to the estimated population prior to
37 the period of intensive, unregulated harvest. Like other crocodylians, the harvest simulations
38 showed the viability of the population is highly sensitive to adult survival rates. The
39 estimated population should be able to sustain an annual harvest of up to 135 500 eggs if the
40 harvest of large crocodiles remain small (<500 per year). *Conclusions*; While egg harvest
41 has little impact on population size and structure, population size is sensitive to adult harvest.
42 *Implications*; Crocodile populations are highly sensitive to adult survival, which needs to be
43 taken into account when considering future harvest scenarios.

44

45 Key words

46 carnivore, density dependence, human-wildlife conflict, matrix population model, stage-
47 based, sustainable

48

49 Running head (<50 characters)

50 Crocodile population and harvest simulations

51

52 **Introduction**

53 Populations of large carnivores are often persecuted to protect humans or livelihoods and are
54 subject to conservation programs to protect them from extinction (Weber and Rabinowitz
55 1996; IUCN 2014). However, there are few documented cases where once endangered
56 carnivore populations have shown a recovery substantial enough to allow regulated
57 commercial exploitation or necessitating management intervention to reduce populations in
58 order to protect other values (Treves and Karanth 2003; Treves *et al.* 2006). Saltwater
59 crocodiles *Crocodylus porosus* in the Northern Territory, Australia are one such example. By
60 1971, 26 years of **unregulated intensive hunting of crocodiles in all sizes except for eggs** had
61 reduced the population to an estimated 3000-5000 animals and there were serious concerns
62 about the long-term survival of the species in the wild (Webb *et al.* 1984). The species was
63 formally protected in 1971 for the specific purpose of allowing the remaining population to
64 recover without direct management intervention. Population monitoring commenced in 1975
65 (Messel *et al.* 1981; Webb *et al.* 1984) and has continued until the present with only minor
66 gaps in the record (Webb *et al.* 2000; Fukuda *et al.* 2011). The population has recovered
67 steadily since 1971 and the objective of management has consequently shifted from one of
68 conservation (Messel *et al.* 1981) to sustained-yield harvesting with limited population

69 control in some situations (Webb and Manolis 1993; Saalfeld *et al.* 2015; Saalfeld *et al.*
70 2016). Population control involves the removal of some crocodiles to reduce human-
71 crocodile conflict around human settlements (Nichols and Letnic 2008; Fukuda *et al.* 2014).
72 The sustained yield harvest strategy adopted incentivises landowner conservation of crocodile
73 populations and habitat on their land by allowing them to use crocodiles for commercial gain
74 (Webb and Manolis 1993). Similar incentive-driven management for conservation benefits
75 has been implemented for other crocodylian species, including American alligators (*Alligator*
76 *mississippiensis*), that have much larger populations than *C. porosus* in Australia (Elsley and
77 Woodward 2010), and Nile crocodiles (*Crocodylus niloticus*) (Fergusson 2010). There are
78 now significant industries around crocodile-based tourism (Ryan 1998) and the commercial
79 farming of animals for meat and skins (Webb and Manolis 1993; Saalfeld *et al.* 2015). The
80 latter is underpinned by the harvest in the Northern Territory of wild eggs, which are
81 incubated on crocodile farms, and a small harvest of adult animals to supplement breeding
82 stock on crocodile farms and for direct production of skins and meat. Customary use of
83 saltwater crocodiles by indigenous people still occurs, as it has for tens of thousands of years
84 (Webb *et al.* 1984; Lanhupuy 1987).

85
86 The approach taken to date to ensure the sustainability of wild harvests has been to set a
87 conservative quota for eggs and free-living crocodiles and monitor the impact on the
88 population through standardised surveys (Leach *et al.* 2009; Fukuda *et al.* 2011). There has
89 been no attempt to investigate what level of harvest the current population could sustain and
90 the relative impacts on the population of harvesting eggs as opposed to harvesting or
91 removing wild adult crocodiles. To address this gap, we built a series of matrix population
92 models to simulate changes in the population size and structure under different levels of
93 harvest intensity of both eggs and wild crocodiles for 70 years since protection (1971-2047).
94 We incorporated environmental stochasticity and density-dependent factors into these
95 models. This allowed us to explore 1) whether the controlled harvest of eggs and adults since
96 protection has had an adverse effect on population size and structure, and 2) the effect of
97 future harvest scenarios on population size and structure by adjusting harvest levels of both
98 eggs and adults. .

99

100 **Methods**

101 *Study area*

102 *Crocodylus porosus* is distributed across the northern coastal region of the Northern
103 Territory, Australia between 128°E and 138°E , mostly north of 17°S (Fig. 1), where it
104 inhabits a range of freshwater and saline water bodies (Webb and Manolis 1989; Fukuda *et al.*
105 *al.* 2007). The climate is monsoonal with distinct wet (November-April) and dry (May-
106 October) seasons. In Darwin, mean monthly ambient temperatures at 1500 hr range from 19.3
107 to 33.3 °C, and 93% of the 1738 mm annual rainfall occurs during the wet season, causing
108 flooding and the expansion of perennial wetlands (Bureau of Meteorology 2020). The tidal
109 rivers and associated floodplains that constitute a core habitat for *C. porosus* typically contain
110 freshwater during the wet season, with a salt wedge moving progressively upstream during
111 the dry season (Fukuda and Cuff 2013). The study area contains 12 large tidal rivers that have
112 been consistently monitored for crocodiles since the 1970s (Messel *et al.* 1981; Webb *et al.*
113 2000; Fukuda *et al.* 2011), eight of which are subject to the regulated, commercial harvest of
114 both eggs and wild crocodiles (Saalfeld *et al.* 2015; Saalfeld *et al.* 2016).

116 *Demographic model*

117 We built a series of matrix population models for saltwater crocodiles. This modelling
118 technique offers a mechanism for simulating the possible impact of harvest at different levels
119 on the absolute abundance and structure of a population over a projected length of time
120 (Caswell 2001; Morris and Doak 2002; Pople 2004). We used MATLAB version R2012b
121 (MathWorks, Natick, USA) to build the demographic models and our terminology follows
122 Morris and Doak (2002).

124 We followed the following steps in constructing the matrix population models and
125 conducting simulations with these models:

- 126 1. Define the life/size stages for *C. porosus*
- 127 2. Quantify the matrix model elements for the different life/size stages
- 128 3. Use the initial deterministic model to estimate the structure of the population at the
129 time of protection (1971) given the population estimate at this time
- 130 4. Incorporate environmental stochasticity in regards to breeding success in the model
- 131 5. Incorporate aspects of density dependence in the model
- 132 6. Evaluate **current harvest** effects by comparing models with and without harvest
133 offtake for the period 1971-2017

134 7. Explore effect of future harvest scenarios over the period 2018-2047 by adjusting
135 harvest levels used in the model and incorporating environmental stochasticity on
136 population size and structure

137 8. Examine elasticity in demographic parameters used in the model

138 Aspects of these steps are described below.

139

140 *Define the life/size stages for C. porosus*

141 Crocodylian populations are commonly structured on the basis of morphological stage or size
142 (Nichols 1987; Dunham *et al.* 2014) and these structured population models can be sensitive
143 to the number and width of the stages selected (Wallace *et al.* 2013). To be consistent with
144 the life stages used in the management programs for *C. porosus* in the Northern Territory and
145 in other literature (Webb *et al.* 1984; Leach *et al.* 2009), we defined four classes for both
146 males and females to parameterise the models: eggs (N_1), hatchlings (N_2 ; hatched crocodiles
147 with total length [TL] <0.6 m), juveniles (N_3 , TL 0.6-2.1 m), and adults (N_4 , TL >2.1 m). We
148 assumed that all ovipositioned eggs enter N_1 and surviving hatchlings enter N_2 after the
149 typical incubation period of 90 days (Webb *et al.* 1984). These newborn hatchlings exceed
150 0.6 m within a year (Webb and Manolis 1989) and enter N_3 . Survivors from N_3 enter N_4 when
151 exceeding 2.1 m, usually after several years.

152

153 *Quantify the matrix model elements for the different life/size stages*

154 Given that the reproduction of *C. porosus* is typically confined to three to five months each
155 year (Webb and Manolis 1989; Webb 1991), we set the theoretical census of this 'birth pulse'
156 population at the time of oviposition (thus post-breeding census) so that one projection of the
157 matrix would generate changes in each of the stages immediately after reproduction in a
158 consecutive year. For the survival of N_1 , we used the probability of eggs hatching
159 successfully.

160

161 Following the definitions of Caswell (2001) and Morris and Doak (2002), we constructed a
162 life cycle diagram (Fig. 2), for which we quantified the matrix elements, using the relevant
163 vital rates (Table 1), derived from the literature and previous empirical datasets mentioned
164 below. The transition rate (G_i) is the probability of surviving individuals in stage i that can be
165 expected to enter stage $i+1$ in a year, and was estimated as $G_i = \sigma_i \gamma_i$, where σ_i is annual
166 survival at stage i , and γ_i is growth probability that an individual at stage i would grow to
167 enter stage $i+1$. For example, σ_1 is the survival of eggs (N_1) until they hatch and σ_2 is the

168 survival of hatchlings (N_2) to one year after hatching (Webb 1977; Messel *et al.* 1981, p.198;
169 Webb *et al.* 1984). The annual survival for juveniles (N_3) - σ_3 , was set as the annual survival
170 for crocodiles in 0.6-1.8 m (2-6 ft) as given in Webb *et al.* (1984) based on repetitive surveys
171 in a number of rivers by Messel *et al.* (1981). The annual survival for adults (N_4) - σ_4 , was set
172 at 0.99 for 12-60 year-old crocodiles and that for 60-70 year-old crocodiles at 0.95 as
173 suggested by Webb *et al.* (1984). The growth probability (γ_i) was estimated as $\gamma_i = T_i^{-1}$ where
174 T_i is the average duration of the stage i . The persistence rate (P_i) is defined as the probability
175 of individuals in stage i remaining in that stage next year, and was estimated as $P_i = \sigma_i(1 - \gamma_i)$.
176 We assumed that there is no persistence with eggs, because all eggs hatch or die before they
177 enter N_2 . Similarly, individuals in N_2 do not have persistence, because all hatchlings die or
178 enter N_3 within a year. We assumed that estimates for these parameters did not differ between
179 males and females (thus, we had a single projection matrix for both sexes). Although the
180 duration of the stage N_1 (T_1) is less than 1 year, the growth probability (γ_1) for N_1 was set at 1
181 because all hatched eggs enter the next stage as hatchlings within a year. γ_3 is the reciprocal
182 of the duration of juveniles [the age of crocodiles at 2.1m was estimated at 10.32 years for
183 female and 8.29 years for males, derived from the equations in Webb and Messel (1978a) and
184 Webb *et al.* (1978) modified with unpublished results (G. Webb, Wildlife Management
185 International (WMI)). The duration of the juvenile stage is 8.31 years (the mean of male and
186 female minus the duration of hatchling)]. γ_4 was set as 0, because there is no transition after
187 the adult stage.

188

189 Reproduction in juvenile (N_3) crocodiles rarely occurs in the wild (Webb and Manolis 1989),
190 thus reproduction (F_i) was considered only for N_4 (Fig. 2). Note that another recruitment
191 component that would have been produced by individuals that just entered N_4 from N_3 as a
192 post-breeding projection (Kendall *et al.* 2019) **was not included in the model as these were**
193 **sexually immature females (see below)**. F_4 was estimated as $F_4 = P_4 m_4$ where m_4 is the
194 number of female births (embryos) in N_1 per breeding adult female in N_4 per year and P_4 is
195 the survival of individuals in N_4 accounted as parents in a birth-pulse population. m_4 was
196 calculated from the average clutch size, 53.1 (Webb and Manolis 1989) and sex ratio, 0.5
197 (Webb *et al.* 1977; Webb and Messel 1978b). Like some other reptile species, the sex of *C.*
198 *porosus* embryo is determined by the incubation temperature and the ratio could be skewed
199 towards one sex, depending on the environmental conditions during incubation. However,
200 Webb *et al.* (1984) considered that a 50:50 ratio would be a reasonable estimate based on

201 reports from early studies (Webb *et al.* 1977; Webb and Messel 1978b), and WMI (2007)
202 later supported this view based on their field observations over 28 years.

203

204 Because, in the wild, females attain maturity at about 2.3 m and males at 3.3 m (Webb *et al.*
205 1984; Webb and Manolis 1989), N_4 includes some sexually immature females (2.1-2.3 m)
206 and males (2.1-3.3 m). Moreover, females appear to become sexually active and start nesting
207 only when a social opportunity (such as access to limited nesting sites) occurs (WMI 2007;
208 G. Webb, WMI, unpublished results). These sexually immature and reproductively inactive
209 individuals were accounted for in the density-dependent estimate of the fertility parameter
210 below.

211

212 *Structure of the population at the time of protection (1971) given the population estimate at*
213 *this time*

214 We fitted the matrix elements into the initial deterministic (non-stochastic), density-
215 independent projection matrix to obtain an initial estimate of the structure of the population at
216 the time of protection (1971). As the population was structured by life stages on the basis of
217 size rather than age, we used the standard size-classified population matrix (Lefkovich
218 matrix; Caswell 2001) to generate the right eigenvector (w_1), which is the percentage of each
219 life stage in the population in 1971 (Table 2). Using these proportions and setting the number
220 of non-hatchlings (N_3+N_4) in 1971 at 4000 (derived from Webb *et al.* (1984) and Richardson
221 *et al.* 2002), we estimated the number of individuals in stages N_1 to N_4 in 1971. We used
222 these estimates as the initial population vector (w_0) for later population simulations.

223

224 *Environmental stochasticity*

225 Annual variability in climate affects the ability of *C. porosus* to exploit local environments in
226 various ways, which ultimately influences their reproductive effort and success (Nichols
227 1987; WMI 2007). Breeding of *C. porosus* occurs in the wet season (Nov-Apr), nesting tends
228 to be reduced after a prolonged dry season and rainfall at the start of the wet season triggers
229 courtship and breeding (Webb 1991; Fukuda and Saalfeld 2014). We incorporated this
230 environmental stochasticity into our model by adjusting reproduction (F_4) according to the
231 extent and timing of wet season rainfall between 1971-2019 (Fig. 3). We indexed the severity
232 of the dry seasons as the number of months between consecutive wet seasons with <100 mm
233 rainfall using data for Darwin (Bureau of Meteorology 2020). This ranged from 5 to 10
234 months (mean = 7.6 ± 1.06), and so we calculated the probability of it being dry for a long (≥ 9)

235 months; 20% of years), moderate (7-9 months; 35%) or short (≤ 7 months; 45%) period and,
236 based on long-term nest monitoring data (WMI 2007), applied a -15% and +15% correction
237 to the extent of nesting for long and short dry seasons, respectively. In population simulations
238 beyond 2019, the duration of each dry season was selected from a weighted random
239 probability table.

240

241 We did not ~~include-account for~~ the possible effect of environmental stochasticity on the
242 survival of eggs. ~~A~~ although it is known that nests are prone to flooding and that this causes
243 mortality (Webb *et al.* 1977; Webb *et al.* 1983), ~~due to~~ no empirical data are available on
244 either the frequency of flooding or variation in the mortality of eggs as a result of
245 flooding. ~~the variation in this parameter. Furthermore, we assumed that, once hatched, the~~
246 survival of a crocodile would not be subject to large fluctuation among years and so did not
247 factor in an effect of The environmental stochasticity ~~was also not included on~~ the survival
248 of the other classes. ~~as we assumed that, once hatched, the survival of a crocodile would not~~
249 ~~be a subject to large fluctuation among years.~~ We also did not consider demographic
250 stochasticity in our modelling because it would generate evident variation in the vital rates
251 only in a small population (< 20 individuals in a stage; (Morris and Doak 2002) while our
252 population was much larger (> 1000 individuals in N_4 of the initial population; Table 2).

253

254 *Density-dependence*

255 While there is strong evidence that the population dynamics of wild *C. porosus* are subject to
256 a suite of density-dependent factors (Webb *et al.* 1984; Webb and Manolis 1992; Bradshaw *et*
257 *al.* 2006), few studies have successfully incorporated density-dependence in crocodylian
258 population models. We considered two different types of density-dependence: intra-stage
259 density dependence and inter-stage density dependence. Intra-stage dependence accounts for
260 the survival of individuals in one stage as a function of the density of individuals in that
261 stage. Females exhibit nest defence to protect their eggs (N_1) and they do not excavate the
262 nests of other females (Webb and Manolis 1989), and thus no density-dependence in the
263 mortality of N_1 was considered. However, hatchling (N_2) survival declines as the number of
264 hatchlings recruiting into a population increases (Webb and Manolis 1992), which is density-
265 dependence at an intra-stage level. There are a number of intra-stage density-dependent
266 influences in N_4 . Dominant males engage in combat with other males, leading to injuries and
267 death (Webb and Manolis 1989), which is a density-dependent influence on survival. The
268 proportion of adult-sized females that start nesting is constrained by the number of females

269 already nesting in a site (Webb *et al.* 1977; Hines and Abercrombie 1987). There is a building
 270 population of socially-recessive individuals not nesting despite being biologically capable of
 271 reproducing (WMI 2007), and if a nesting female dies another quickly takes her place. This
 272 leads to an intra-stage density-dependence in the fertility parameter.

273

274 The other type of density-dependence is ‘inter-stage’. Larger saltwater crocodiles prey on
 275 smaller individuals (Webb *et al.* 1984; Webb and Manolis 1989) or force them into habitats
 276 where they become subject to higher mortality rates (Webb and Messel 1978b; Messel *et al.*
 277 1981; Nichols and Letnic 2008). Webb and Manolis (1992) demonstrated that the survival of
 278 young juveniles (N_3) was negatively correlated with the total number of larger crocodiles (N_3
 279 and N_4) in a river due to cannibalism and social exclusion. Thus we considered density-
 280 dependent influences on N_3 survival at both intra- and inter-stage levels.

281

282 These intra- and inter-class density-dependencies in survival parameters were incorporated
 283 into the models using the two-parameter Ricker function (Morris and Doak 2002),

284

$$285 \sigma_i(D_{i, i+1}) = \sigma_i(0)\exp(-\beta_i D_{i, i+1})$$

286

287 where $\sigma_i(D_{i, i+1})$ is the annual survival of individuals in stage i as a function of $D_{i, i+1}$, the
 288 density of stage i (intra-class) or $i+1$ (interclass); $\sigma_i(0)$ is the maximum survival in stage i at
 289 low densities; and β_i is a measure of the strength of density-dependence for stage i .

290

291 Morris and Doak (2002) suggested that, if all survival estimates are greater than zero, which
 292 is always the case in this study, the β_i values for the Ricker function can be estimated by
 293 regressing the logarithm of stage-specific survival against abundance over time, as

294

$$295 \log[\sigma_i(D_{i, i+1})] = a + bD_{i, i+1}$$

296

297 where $\sigma_i(D_{i, i+1})$ and $D_{i, i+1}$ are as defined above, the slope of the regression (b) is $-\beta_i$, and the
 298 intercept (a) equals $\log[\sigma_i(0)]$.

299

300 With no time-series survival data for *C. porosus* available in the literature, and conducting
 301 mark-recapture surveys across the study area being impractical, we substituted ‘retention’
 302 rates for survival as done by Webb and Manolis (1992). Retention rate is the abundance of

303 **animals sighted in one year divided by abundance in the previous year.** We assumed that the
304 transition (G_i) and persistence (P_i) of each class was as shown in Table 1 and estimated the
305 retention rates of N_2 , N_3 and N_4 from their relative densities derived from the time-series data
306 (1975-2011) of spotlight surveys in 12 tidal rivers across the study area (Fig. 1; Fukuda *et al.*
307 2011; Fukuda and Saalfeld 2014). Crocodiles were counted using a spotlight at night from a
308 boat travelling along the river at low tide and observed sufficiently closely that TL could be
309 estimated within 0.3 m intervals (Messel *et al.* 1981; Fukuda *et al.* 2013). Crocodiles that
310 could not be approached closely enough to determine size were not included in density
311 estimates and only data from river mainstems were used because those from side-creeks
312 were not consistent among the years.

313
314 For the density term $D_{i,t+1}$, we calculated the density as individuals sighted per square
315 kilometre of river surveyed rather than linear kilometre so that the simulations of the
316 population would be spatially explicit, accounting for the limited area of habitats available in
317 the study area. The extent of the surveyed areas, including the water surface and exposed
318 banks at low tide where most crocodiles spend most of their time (Webb *et al.* 1989), were
319 measured using ArcGIS version 10.2 (ESRI, Redlands, USA).

320
321 Population-wide production of hatchlings is constrained by the availability of nesting habitat
322 (Fukuda *et al.* 2007; WMI 2007), and we modelled this density-dependent factor by the
323 Beverton-Holt equation (Morris and Doak 2002). Unlike the over-compensating density-
324 dependence of survival rates (Ricker function), reproduction should show an asymptotic
325 decrease as the number of adult-size nesting females increases in this function. After
326 reproduction ceases at the asymptote, the total number of eggs will not decrease any lower
327 than those produced in the available nesting sites even if the number of adult-sized nesting
328 females continues to increase. We parameterised the Beverton-Holt equation as $f(d) =$
329 $f(0)/(1+\beta_5d)$ where $f(d)$ is the proportion of females in N_4 that breed each year as a function of
330 the density of sexually-matured females (d), $f(0)$ is the maximum proportion of females in N_4
331 that breed every year, and β_5 is a constant which measures the strength of density dependence
332 in the fertility parameter $f(d)$.

333
334 We accounted for sexually-immature (non-breeding) females (2.1-2.3 m) in N_4 by omitting
335 the recruitment component that would have been produced by individuals that just entered N_4
336 from N_3 and reproduced before the post-breeding census (see Fig. 2). On the basis of the

337 growth rates of females in this 2.1-2.3 m sub-class (Webb *et al.* 1978), we assumed that
338 sexually immature females **were all in their first year in N_4** and would reach 2.3 m in the
339 following year.

340

341 We could not estimate the value of the constant β_5 empirically because there were very few
342 data relating the density of crocodiles to the proportion of females nesting every year.
343 Instead, we used an iterative process to determine an appropriate value of β_5 . As a first step in
344 this process, we considered reasonable values for $f(d)$ as follows: 1971- 1.0 at protection;
345 1980-1989- 0.8; 2000-2010- 0.5 of females in N_4 based on the long-term observations at the
346 Adelaide River, which is one of the major breeding sites in the study area (Webb *et al.* 1984;
347 Webb *et al.* 1989; WMI 2007, G. Webb, WMI, unpublished data). We then varied β_5 over the
348 range 0.1-0.9 in 0.05 increments, solving the Beverton-Holt function for $f(d)$ using the 40
349 (1971-2011) values for d simulated from the structured models (Fig. 4). We visually
350 compared the modelled values for $f(d)$ to the reasonable values for each value of β_5 and
351 obtained the best match at 0.45 (Fig. 5). We used R version 2.15.2 (R Foundation Statistical
352 Computing, Vienna, Austria) to estimate all density-dependence parameters.

353

354 Although *C. porosus* is capable of long distance movements between river systems along
355 coasts (Read *et al.* 2007; Campbell *et al.* 2010; Campbell *et al.* 2013), the extent and patterns
356 of movement to and from the study area is poorly understood. Given that the favourable
357 habitat in the Northern Territory is distinctively bounded by less favourable habitat on the
358 western and eastern boundaries (Fukuda *et al.* 2007), we assumed that immigration and
359 emigration rates were low in the study area and the model treats crocodiles in the Northern
360 Territory as a closed population.

361

362 *Current harvest effects*

363 *C. porosus* in the Northern Territory has been subject to managed harvest programs since
364 1983 (Webb *et al.* 1984). The major form of the harvest is egg collection for commercial
365 farming, but juveniles (N_3) and adults (N_4) are also harvested for breeding or direct
366 production of skins and meat (Fig. 6). As a trial ranching program, 298 eggs were first taken
367 in 1983 (Webb *et al.* 1984) and the quota has increased greatly since then (90 000 eggs in
368 2017, Leach *et al.* 2009; Saalfeld *et al.* 2016). The harvest of juveniles and adults started in
369 1997 and has remained far below the modest quota (1200 for N_3 and N_4 together in 2017). In
370 addition, crocodiles posing risks to people or domestic animals near human settlements are

371 considered ‘problem crocodiles’ and have been removed from the wild since 1977.
372 Hatchlings (N_2) are rarely caught or removed for any purpose (Leach *et al.* 2009). Between
373 1977 and 2017, a total of 799 657 eggs, 3612 crocodiles in N_3 , and 4987 crocodiles in N_4
374 were harvested or removed from the wild. To simulate the effects of post-protection human
375 intervention on the population size and structure, we incorporated these numbers into the
376 model as additional mortality.

377
378 In *C. porosus*, mortality in eggs that is caused by flooding in the peak of the nesting season
379 (January to March) can be as high as 0.75. Furthermore, **flood related mortality varies**
380 **according to habitat type**. Flooding occurs at the time of year when most egg harvesting
381 occurs across the Northern Territory. This means that harvesting removes many eggs that
382 would otherwise be lost to flooding. As a result, mortality from direct harvesting is not
383 wholly additive, but partially compensatory to natural mortalities as occurs in many
384 vertebrates (Morris and Doak 2002; Mills 2012). We accounted for this effect by estimating
385 the proportion of harvested eggs that would have been lost to the flooding if not collected.

386
387 Generally there are three types of nesting habitat in the study area (Webb and Manolis 1989);
388 Type 1 = spring-fed freshwater swamps draining to tidal rivers, Type 2 = upstream freshwater
389 swamps, and Type 3 = floodplains adjoining mangrove-lined tidal rivers. In Type 1 habitats,
390 mortality due to flooding is relatively low, but in Type 2 and 3 habitats flooding due to both
391 rain and tidal effects results in the highest egg mortality (Webb 1977; Hill and Webb 1982;
392 Fukuda and Saalfeld 2014). From the empirical data associated with the long-term harvest
393 (WMI 2007, G. Webb, WMI, unpublished results), we assumed that 25% of harvested eggs
394 would have been flooded if not collected in the Type 1 habitats, 50% in Type 2 and 60% in
395 Type 3. The percentage of each nesting habitat type was estimated from digitised topographic
396 data as 15% of the total nesting habitat (Type 1), 45% (Type 2) and 40% (Type 3). Overall,
397 we estimated 50.3% of the eggs harvested each year would have been lost to flooding and
398 49.7% therefore constituted additional mortality due to harvest.

399
400 Harvest effects were incorporated into the model by reducing the survival (σ) of each stage in
401 each year. The survival of the harvested stage i was estimated as $\sigma_i = (1-H/N_i) \sigma_i$ (*no harvest*)
402 where H is the number of individuals harvested, N_i is the number of individuals before
403 harvest, and σ_i (*no harvest*) is the maximum survival of size class i when there is no harvest.

404 For N_2 , N_3 and N_4 , σ_i (*no harvest*) is the survival when density-dependence is incorporated as
405 described above.

406

407 To examine the effect of the **current harvest** (1983-2017), we ran paired matrix models for
408 years 1 to 40 (to mimic the period 1972-2017). The first model assumed no harvest and the
409 other incorporated the commercial harvest and problem crocodile removal for each year.

410

411 *'Future' harvest scenarios*

412 We explored different harvest scenarios for another 30 years (mimicking 2018-2047) on the
413 basis of the model that incorporated the actual harvest of eggs (1983-2017) and crocodiles in
414 N_3 and N_4 (1997-2017). We examined different harvest scenarios by varying the harvest
415 levels of eggs and crocodiles in N_4 , because these two classes are the most important targets
416 for commercial harvest and for improving public safety (Webb and Manolis 1993; Fukuda *et al.*
417 *et al.* 2014; Saalfeld *et al.* 2015). We assumed that the annual harvest intensity of crocodiles in
418 N_3 would be constant at 591 (400 as in **current harvest** quota + 191 as problem crocodiles)
419 and the annual harvest of crocodiles in N_4 would include 209 problem crocodiles in all cases.
420 These number of problem crocodiles in N_3 and N_4 were determined based on 2923 problem
421 crocodiles caught between 1994 and 2011, of which 47.7% were <2.1 m TL (N_3) and 52.3%
422 were >2.1 m TL (N_4). We assumed the number of problem crocodiles would level out at 400
423 per year for 2018-2047 in the simulation. Given the projected growth of the commercial
424 crocodile industry, and greater risks to human safety from crocodiles as human population in
425 the northern NT increase, it is likely that the harvest of eggs and crocodiles in N_4 will
426 increase (Leach *et al.* 2009; Saalfeld *et al.* 2016). We therefore simulated four potential
427 scenarios, with the annual harvest of eggs being constant at 20% of the saturation at 2017
428 (equivalent to 135502 eggs at year 0) while achieving different population sizes by adjusting
429 the annual harvest of crocodiles in N_4 . These simulation models over the next 30 years were
430 *S1*: maintain the non-hatchling population with no decline (0% change); *S2*: maintain the
431 population without any significant decline (<5% change); *S3*: reduce the population by
432 approximately 25% and then maintain this level; and *S4*: reduce the population by
433 approximately 40% and then maintain this level. We also illustrated the impact of these
434 harvest scenarios in terms of the rate of change in crocodiles N_4 as well as the number of
435 crocodiles in N_3 and N_4 (non-hatchlings).

436

437 In all the simulations, we ran each model with 500 iterations so that each simulation would
438 randomly pick a projection matrix with the different levels of the environmental stochasticity
439 in F_4 , but with the consistent density-dependence in f , σ_2 , σ_3 , and σ_4 . The mean and standard
440 error of the number of individuals in each class was then calculated for each year.

441

442 *Elasticity*

443 To compare the influence of different demographic parameters used in the simulations of
444 population recovery, particularly the stage-specific survival estimates and β_i values, we
445 calculated the elasticity of the demographic parameters. While sensitivity reflects how
446 sensitive population growth rate (λ) is to changes in a demographic parameter, elasticity
447 allows the sensitivities of λ to different parameters to be directly compared with each other
448 (Grant and Benton 2000; Tucker 2001; Morris and Doak 2002). We calculated the elasticity
449 (e) as the partial derivative (∂) of λ with respect to each demographic parameter (x) as $e =$
450 $(\partial \log \lambda) / (\partial \log x)$. Although this equation assumes that the population is deterministic, these
451 elasticities can be interpreted with caution for a stochastic population (Morris and Doak
452 2002), provided the stochastic changes in the parameters are not large, which is the case in
453 this study.

454

455 **Results**

456 The survey data from the period in which the population was recovering rapidly (1975-2017),
457 indicated that survival in N_2 and N_4 was significantly negatively correlated with the
458 increasing density of crocodiles in N_2 and N_4 respectively ($P < 0.001$). Density dependence for
459 survival of N_2 as a function of the density of crocodiles in N_2 was much stronger than that for
460 survival in N_4 as a function of the density of crocodiles in N_4 (Table 3). On the other hand,
461 survival of crocodiles in N_3 did not show a significant relationship with density in any other
462 stages or combinations of them, including non-hatchlings ($N_3 + N_4$). Thus, no changes in the
463 survival of crocodiles in N_3 as a function of the densities of crocodiles in N_3 and N_4 were
464 assumed in the following population simulations ($\beta_3 = 0$).

465

466 The simulations of the harvested and non-harvested populations for year 1-46 (1972-2017)
467 showed very similar asymptotic trajectories in which the population increased exponentially
468 in the first phase (the 1970s and early 1980s) and then linearly in the second stage (late
469 1980s), with the rate of increase progressively slowing after the 1990s and approaching zero

470 after the 2000s (Fig. 7). Population size and the proportion of individuals in each stage were
471 similar between the harvested and non-harvested models (Table 4). The harvested population
472 model estimated the population for 2017 as $102\,515 \pm 88.16$ non-hatchlings.

473

474 To achieve the different management scenarios for years 41-70 (S1-S4 in Fig. 8), the
475 simulations used different percentages of crocodiles in N_4 as annual harvest quotas. To
476 stabilise the non-hatchling portion of the population over the period, annual harvests of
477 crocodiles in N_4 would need to be 1% of crocodiles in N_4 estimated at each year (equivalent
478 to 435 adults for 2017) (S1). To achieve a <5% decline in the non-hatchling population over
479 the period, with annual harvests of N_4 crocodiles would have to increase to 5% of N_4
480 individuals estimated each year (equivalent to 2175 adults in 2017) (S2). To reduce the
481 population by 25%, the quota needed to increase to 16% of crocodiles in N_4 estimated each
482 year (equivalent to 6960 adults in 2017) (S3). To reduce the population by 40%, 22% of
483 crocodiles in N_4 estimated each year (equivalent to 9570 adults in 2017) would need to be
484 harvested annually (S4). Under all the scenarios, the harvest of eggs remained 20% of N_1
485 estimated each year (equivalent to 135502 eggs). The rates of change in the number of
486 crocodiles in N_4 stabilised at -0.01, -0.15, -0.48, and -0.62 under S1-S4, respectively.

487

488 The elasticity of the survival estimates applied for stages N_1 , N_2 , N_3 and N_4 were 0.09, 0.11,
489 0.21 and 0.68 respectively, indicating that survival rates among larger individuals have a very
490 strong influence on population growth rate (λ) predicted from the model. The elasticities of
491 the fertility parameter, applicable only to N_4 , and the growth probability of N_3 , did not have a
492 strong influence on λ (0.13 for f and 0.07 for γ_3). Similarly, the measures for density
493 dependence had a minor influence on λ (elasticities -0.08, -0.04 and -0.04 for β_2 , β_4 and β_5 ,
494 respectively) with the expected, negative effects on λ .

495

496 **Discussion**

497 *Effect of harvest*

498 The models described in this paper indicate that the **current harvest** of eggs and the removal
499 of crocodiles in N_3 and N_4 in the Northern Territory for commercial use and public safety
500 were conservative, well below any maximum sustainable harvest. The simulations showed
501 little difference in the rate of increase in abundance and size structure of the population

502 regardless of whether the real harvests that took place were included or excluded, indicating
503 that harvests were both sustainable and demonstrably benign.

504

505 The relatively minor impact of the 1983-2017 harvest in the models indicates that the
506 apparent stabilisation of the population in recent years is not a result of this harvest. Survey
507 data indicate that the stabilisation of abundance (sighting density) has occurred in both
508 harvested and unharvested rivers (Fukuda *et al.* 2011). This suggests that local populations
509 are limited by environmental factors such as the availability of suitable nesting habitats, as
510 suggested by previous studies (Fukuda *et al.* 2007; Fukuda and Cuff 2013).

511

512 In the Northern Territory, monitoring programs to assess the status of *C. porosus* over time
513 started soon after protection (1971) and provided time-series data on changing population
514 abundance and size structure spanning more than four decades (1975-2017). They clearly
515 documented the recovery of a severely depleted population (Messel *et al.* 1981; Webb *et al.*
516 2000; Fukuda *et al.* 2011). The asymptotic pattern of population recovery simulated in this
517 study is consistent with these monitoring data, that the intrinsic increase during the 1980s
518 slowed drastically after the 1990s towards a ceiling in the 2000s (Fig. 7 and Fukuda *et al.*
519 (2011)). This highlights the species ability to increase rapidly if protected in habitats suitable
520 for breeding. In most of the global range of the species, local populations are highly depleted
521 (Webb *et al.* 2010), but our results indicate their potential to recover if given the opportunity.

522

523 *Current population size and structure*

524 Given the dichotomous nature of human perception of crocodiles, as culturally-important, an
525 iconic wild species and a commercially important natural resource on the one hand, and a
526 serious risk to humans and livestock on the other, the absolute abundance of the wild
527 population has always been of interest to the public and to management agencies (Webb *et al.*
528 1984; Fukuda *et al.* 2014). Our model simulations predicted approximately 102 500 non-
529 hatchlings (crocodiles in N_3 and N_4) in the Northern Territory in 2017, of which 42.5% are
530 crocodiles in the largest size class (N_4 , >2.1 m TL). Adult males could represent as much as
531 50% of the N_4 cohort, although the proportion of very large adult males (>4.2 m TL),
532 considered particularly dangerous for people and livestock (Fukuda *et al.* 2015), would be a
533 relatively small component of this group (probably <2% of the non-hatchlings). This is
534 consistent with the very low sighting rates of very large crocodiles in historical population
535 monitoring surveys (Webb and Messel 1979; Messel *et al.* 1981). However, this situation can

536 be expected to change in a population approaching carrying capacity, where the proportion of
537 large individuals is expected to increase relative to small individuals (Webb *et al.* 2000;
538 Fukuda *et al.* 2011; Saalfeld *et al.* 2016). An early indication of this is the increasing
539 proportion of crocodiles larger than 1.8 m TL over the period that the population has been
540 monitored (Fukuda *et al.* 2011; Fukuda *et al.* 2014). The current estimated population is now
541 approaching the size suggested for the 'natural' wild population before uncontrolled hunting
542 (around 100 to 120 000 individuals, Webb *et al.* 1984; Fukuda *et al.* 2014).

543

544 *'Future' harvest scenarios*

545 The harvest simulations presented here are a first step towards generating hypotheses about
546 the likely impact of future harvest or control scenarios, thereby providing a robust theoretical
547 framework for advancing adaptive management. Our modelling suggests that the wild
548 population would sustain indefinitely an annual harvest of 20% of eggs and 1% of crocodiles
549 in N_4 estimated each year over 30 years. These levels of harvest, being equivalent to
550 approximately 435 adult crocodiles and 135 500 eggs, are much higher than the documented
551 harvest in 2017 (41 218 eggs and 250 adult crocodiles).

552

553 The viability of crocodylian populations is highly sensitive to adult survival rates (Nichols
554 1987; Tucker 2001; Dunham *et al.* 2014; Briggs-Gonzalez *et al.* 2017), as for other large
555 predators (Hebblewhite *et al.* 2003; Carroll and Miquelle 2006). In this study, the role of
556 adult harvest was considered in four harvest scenarios with different management objectives
557 (Fig. 8). While egg harvest had little impact on sustainability, for all the scenarios a
558 sustainable population at differing levels was effectively achieved by changing the harvest
559 intensity for N_4 . It should be noted that the number of larger individuals would decline at a
560 higher rate than smaller ones as shown by the rates of decline in crocodiles in N_4 being higher
561 than the controlled declines in non-hatchlings ($N_3 + N_4$) under all the scenarios. This is not to
562 say that the harvest of large individuals is not feasible, but the proportionately higher impact
563 of taking adults needs to be taken into account when managing a harvest program. If the
564 harvest of large individuals is to be increased, we recommend that more detailed simulation
565 analysis be undertaken before implementation to robustly estimate the possible impact.
566 Particularly, the random effect of the environmental stochasticity that can drive a population
567 to a level markedly lower or higher than expected (e.g. individual simulations for S3 and S4
568 in Fig. 8) would require regular, comprehensive monitoring after implementation to validate
569 the expected outcome and detect any undesirable impact.

570

571 In this study we relied on static estimates of vital demographic rates garnered from previous
572 studies (eg. Webb *et al.* 1984). **The lack of variations reported from field in some of these**
573 **variable prevented an assessment of the effect of that variation on the dynamics of a**
574 **population.** This also precluded us from using more recently available population modelling
575 approaches such as Integrated Population Modelling (IPM: Kery and Schaub 2011, Schaub
576 and Abadi 2011). IPM combines time series data on population size with corresponding data
577 on demographic rates. However, while such techniques may offer advantages over the
578 approach used here, we expect that it would be difficult to collect the required demographic
579 data on a species like *C. porosus*. A mark recapture study would be logistically challenging
580 and costly while counts of hatchlings are notoriously variable rendering them unsuitable for
581 determining reproductive success.

582

583 *Implications*

584 This study provides evidence to support the view that the harvest of *C. porosus* and their eggs
585 since protection (1971) in the Northern Territory has been benign, with no significant impact
586 on the ongoing recovery of the wild population. Further, the models indicate that even a
587 substantial increase in the egg harvest will have little impact on the population as long as the
588 harvest rates of large (>2.1 m) animals remain low. In providing commercial benefits from
589 crocodiles to landowners, harvesters, and farmers, the sustainable utilisation of crocodiles is
590 thought to be effective in maintaining the ongoing conservation of crocodiles. However,
591 tolerance for crocodile attacks on people or domestic animals is likely to have limits as
592 human population increases, and the Northern Territory government may in future adapt its
593 management approach accordingly. If changes in harvest levels are to be considered, the
594 model presented here can be used as the first-step in assessing the likely impact of any new
595 harvest regime on the crocodile population size and structure over a projected length of time.
596 These matrix population models could also be applied to populations of *C. porosus*
597 elsewhere, or to other crocodylian species, provided that appropriate adjustment to the matrix
598 elements and their vital rates are made, preferably from reliable, long-term population survey
599 data such as presented in this study.

600

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612

613 **References**

- 614 Bradshaw, C. J. A., Fukuda, Y., Letnic, M., and Brook, B. W. (2006). Incorporating known
615 sources of uncertainty to determine precautionary harvests of saltwater crocodiles.
616 *Ecological Applications: A Publication of the Ecological Society of America* **16**,
617 1436–1448.
- 618 Briggs-Gonzalez, V., Bonenfant, C., Basille, M., Cherkiss, M., Beauchamp, J., and Mazzotti,
619 F. (2017). Life histories and conservation of long-lived reptiles, an illustration with
620 the American crocodile (*Crocodylus acutus*). *Journal of Animal Ecology* **86**, 1102–
621 1113. doi:10.1111/1365-2656.12723
- 622 Bureau of Meteorology (2020). Climate Data Online. Available at:
623 <http://www.bom.gov.au/climate/data/index.shtml> [accessed 20 February 2020]
- 624 Campbell, H. A., Dwyer, R. G., Irwin, T. R., and Franklin, C. E. (2013). Home range
625 utilisation and long-range movement of estuarine crocodiles during the breeding and
626 nesting season. *PLoS ONE* **8**, e62127. doi:10.1371/journal.pone.0062127
- 627 Campbell, H. A., Watts, M. E., Sullivan, S., Read, M. A., Choukroun, S., Irwin, S. R., and
628 Franklin, C. E. (2010). Estuarine crocodiles ride surface currents to facilitate long-
629 distance travel. *Journal of Animal Ecology* **79**, 955–964. doi:10.1111/j.1365-
630 2656.2010.01709.x
- 631 Carroll, C., and Miquelle, D. G. (2006). Spatial viability analysis of Amur tiger *Panthera*
632 *tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix
633 in population persistence. *Journal of Applied Ecology* **43**, 1056–1068.
634 doi:10.1111/j.1365-2664.2006.01237.x
- 635 Caswell, H. (2001). ‘Matrix Population Models: Construction, Analysis, and Interpretation’.
636 (Sinauer Associates: Massachusetts, USA.)
- 637 Dunham, K., Dinkelacker, S., and Miller, J. (2014). A Stage-Based Population Model for
638 American Alligators in Northern Latitudes. *The Journal of Wildlife Management* **78**.
639 doi:10.1002/jwmg.688

- 640 Elsey, R. M., and Woodward, A. R. (2010). American alligator *Alligator mississippiensis*. In
641 'Crocodiles. Status Survey and Conservation Action Plan'. (Eds S. C. Manolis and C.
642 Stevenson.) pp. 1–4. (Crocodile Specialist Group: Darwin, Australia.)
- 643 Fergusson, R. A. (2010). Nile Crocodile *Crocodylus niloticus*. In 'Crocodiles. Status Survey
644 and Conservation Action Plan'. pp. 6. (IUCN Crocodile Specialist Group: Darwin,
645 Australia.)
- 646 Fukuda, Y., and Cuff, N. (2013). Vegetation communities as nesting habitat for the saltwater
647 crocodiles in the Northern Territory of Australia. *Herpetological Conservation and*
648 *Biology* **8**, 641–651.
- 649 Fukuda, Y., Manolis, C., and Appel, K. (2014). Management of human-crocodile conflict in
650 the Northern Territory, Australia: review of crocodile attacks and removal of problem
651 crocodiles. *Journal of Wildlife Management* **78**, 1239–1249.
- 652 Fukuda, Y., Manolis, C., Saalfeld, K., and Zuur, A. (2015). Dead or alive? Factors Affecting
653 the survival of victims during attacks by saltwater crocodiles (*Crocodylus porosus*) in
654 Australia. *PLOS ONE* **10**, e0126778. doi:10.1371/journal.pone.0126778
- 655 Fukuda, Y., and Saalfeld, K. (2014). Abundance of saltwater crocodile hatchlings is related to
656 rainfall in the preceding wet season in northern Australia. *Herpetologica* **70**, 439–448.
657 doi:10.1655/HERPETOLOGICA-D-13-00096R3
- 658 Fukuda, Y., Saalfeld, K., Webb, G., Manolis, C., and Risk, R. (2013). Standardised method
659 of spotlight surveys for crocodiles in the Tidal Rivers of the Northern Territory,
660 Australia. *Northern Territory Naturalist* **24**, 14.
- 661 Fukuda, Y., Webb, G., Manolis, C., Delaney, R., Letnic, M., Lindner, G., and Whitehead, P.
662 (2011). Recovery of saltwater crocodiles following unregulated hunting in tidal rivers
663 of the Northern Territory, Australia. *Journal of Wildlife Management* **75**, 1253–1266.
664 doi:10.1002/jwmg.191
- 665 Fukuda, Y., Whitehead, P., and Boggs, G. (2007). Broad-scale environmental influences on
666 the abundance of saltwater crocodiles (*Crocodylus porosus*) in Australia. *Wildlife*
667 *Research* **34**, 167–176. doi:https://doi.org/10.1071/WR06110
- 668 Grant, A., and Benton, T. G. (2000). Elasticity analysis for density-dependent populations in
669 stochastic environments. *Ecology* **81**, 680–693. doi:10.2307/177369
- 670 Hebblewhite, M., Percy, M., and Serrouya, R. (2003). Black bear (*Ursus americanus*)
671 survival and demography in the Bow Valley of Banff National Park, Alberta.
672 *Biological Conservation* **112**, 415–425. doi:10.1016/S0006-3207(02)00341-5
- 673 Hill, R., and Webb, G. (1982). Floating grass mats of the Northern Territory floodplains – an
674 endangered habitat? *Wetlands (Australia)* **2**, 45–50.
- 675 Hines, T. C., and Abercrombie, C. L. (1987). The management of Alligators in Florida, USA.
676 In 'Wildlife Management: Crocodiles and Alligators'. (Eds G. J. W. Webb, S. C.
677 Manolis, and P. J. Whitehead.) pp. 43–47. (Surrey Beatty & Sons, Sydney, the
678 Conservation Commission of the Northern Territory: Darwin, Australia.)

- 679 IUCN (2014). 'The IUCN Red List of Threatened Species. Version 2014.3.' (IUCN Species
680 Survival Commission: Gland, Switzerland.) Available at: www.iucnredlist.org
- 681 Kendall, B. E., Fujiwara, M., Diaz-Lopez, J., Schneider, S., Voigt, J., and Wiesner, S. (2019).
682 Persistent problems in the construction of matrix population models. *Ecological*
683 *Modelling* **406**, 33–43. doi:10.1016/j.ecolmodel.2019.03.011
- 684 Lanhupuy, W. (1987). Australian aboriginal attitude to crocodile management. In 'Wildlife
685 Management: Crocodiles and Alligators'. (Eds G. J. W. Webb, S. C. Manolis, and P.
686 J. Whitehead.) pp. 145–147. (Surrey Beatty & Sons, Sydney, the Conservation
687 Commission of the Northern Territory: Darwin, Australia.)
- 688 Leach, G., Delaney, R., and Fukuda, Y. (2009). 'Management Program for the Saltwater
689 Crocodile in the Northern Territory of Australia, 2009-2014'. (Northern Territory
690 Department of Natural Resources, Environment, the Arts and Sport: Darwin,
691 Australia.)
- 692 Messel, H., Vorlicek, G. V., Wells, G. A., and Green, W. J. (1981). 'Monograph 1. Surveys
693 of the tidal systems in the Northern Territory of Australia and their crocodile
694 populations. The Blyth-Cadell River systems study and the status of *Crocodylus*
695 *porosus* populations in the tidal waterways of northern Australia'. (Pergamon Press:
696 Sydney, Australia.)
- 697 Mills, L. S. (2012). 'Conservation of Wildlife Populations: Demography, Genetics, and
698 Management'. (John Wiley & Sons.)
- 699 Morris, W. F., and Doak, D. F. (2002). 'Quantitative Conservation Biology: Theory and
700 Practice of Population Viability Analysis'. (Sinauer Associates: Massachusetts, USA.)
- 701 Natural Resource Management Ministerial Council [NRMCC] (2009). Code of Practice for
702 the Humane Treatment of Wild and Farmed Australian Crocodiles. Available at:
703 [http://www.environment.gov.au/resource/code-practice-humane-treatment-wild-and-](http://www.environment.gov.au/resource/code-practice-humane-treatment-wild-and-farmed-australian-crocodiles)
704 [farmed-australian-crocodiles](http://www.environment.gov.au/resource/code-practice-humane-treatment-wild-and-farmed-australian-crocodiles) [accessed 3 May 2019]
- 705 Nichols, J. D. (1987). Population models and crocodile management. In 'Wildlife
706 Management: Crocodiles and Alligators'. (Eds G. J. W. Webb, S. C. Manolis, and P.
707 J. Whitehead.) pp. 177–187. (Surrey Beatty & Sons, Sydney, the Conservation
708 Commission of the Northern Territory: Darwin, Australia.)
- 709 Nichols, T., and Letnic, M. (2008). Problem crocodiles: reducing the risk of attacks by
710 *Crocodylus porosus* in Darwin Harbour, Northern Territory, Australia. In 'Urban
711 Herpetology. Herpetological Conservation'. (Eds J. C. Mitchell, R. E. Jung Brown,
712 and B. Bartholomew.) pp. 503–511. (Society for the Study of Amphibians and
713 Reptiles: Salt Lake City, USA.)
- 714 Northern Territory of Australia (2013). Animal Welfare Act. Available at:
715 [http://notes.nt.gov.au/dcm/legislat/legislat.nsf/d989974724db65b1482561cf0017cbd2/](http://notes.nt.gov.au/dcm/legislat/legislat.nsf/d989974724db65b1482561cf0017cbd2/28ae66acac5f957569257bd7000a75f2?OpenDocument)
716 [28ae66acac5f957569257bd7000a75f2?OpenDocument](http://notes.nt.gov.au/dcm/legislat/legislat.nsf/d989974724db65b1482561cf0017cbd2/28ae66acac5f957569257bd7000a75f2?OpenDocument) [accessed 17 January 2014]
- 717 Pople, A. (2004). Population monitoring for kangaroo management. *Australian Mammalogy*
718 **26**, 37–44.

- 719 Read, M. A., Grigg, G. C., Irwin, S. R., Shanahan, D., and Franklin, C. E. (2007). Satellite
720 tracking reveals long distance coastal travel and homing by translocated estuarine
721 crocodiles, *Crocodylus porosus*. *PLoS ONE* **2**, e949.
722 doi:10.1371/journal.pone.0000949
- 723 Ryan, C. (1998). Saltwater crocodiles as tourist attractions. *Journal of Sustainable Tourism* **6**,
724 314–327. doi:10.1080/09669589808667319
- 725 Saalfeld, K., Fukuda, Y., Duldig, T., and Fisher, A. (2016). ‘Management Program for the
726 Saltwater Crocodile in the Northern Territory of Australia, 2016-2020’. (Northern
727 Territory Department of Environment and Natural Resources: Darwin, Australia.)
728 Available at: [https://nt.gov.au/__data/assets/pdf_file/0007/443581/crocodile-](https://nt.gov.au/__data/assets/pdf_file/0007/443581/crocodile-management-program.pdf)
729 [management-program.pdf](https://nt.gov.au/__data/assets/pdf_file/0007/443581/crocodile-management-program.pdf)
- 730 Saalfeld, K., Fukuda, Y., Duldig, T., and Fisher, A. (2015). ‘Wildlife Trade Management
731 Plan for the Saltwater Crocodile (*Crocodylus porosus*) in the Northern Territory of
732 Australia, 2016-2020’. (Northern Territory Department of Land Resource
733 Management: Darwin, Australia.)
- 734 Treves, A., and Karanth, K. U. (2003). Human-carnivore conflict and perspectives on
735 carnivore management worldwide. *Conservation Biology* **17**, 1491–1499.
736 doi:10.1111/j.1523-1739.2003.00059.x
- 737 Treves, A., Wallace, R. B., Naughton-Treves, L., and Morales, A. (2006). Co-managing
738 human–wildlife conflicts: a review. *Human Dimensions of Wildlife* **11**, 383–396.
739 doi:10.1080/10871200600984265
- 740 Tucker, A. D. (2001). Sensitivity analysis of stage-structured demographic models for
741 freshwater crocodiles. In ‘Crocodilian Biology and Evolution’. (Eds G. C. Grigg, F.
742 Seebacher, and C. E. Franklin.) pp. 349–363. (Surrey Beatty & Sons: Sydney,
743 Australia.)
- 744 Wallace, K., Leslie, A., and Coulson, T. (2013). Re-evaluating the effect of harvesting
745 regimes on Nile crocodiles using an integral projection model. *The Journal of Animal*
746 *Ecology* **82**, 155–165. doi:10.1111/j.1365-2656.2012.02027.x
- 747 Webb, G. J. W. (1977). Chapter 14. The natural history of *Crocodylus porosus* Habitat and
748 Nesting. In ‘Australian Animals and their Environment’. (Eds H. Messel and S.
749 Butler.) pp. 239–284. (Shakespeare Head Press: Sydney, Australia.)
- 750 Webb, G. J. W. (1991). The influence of season on Australian crocodiles. In ‘Monsoonal
751 Australia - Landscape, Ecology and Man in the Northern Lowlands’. (Eds M. G.
752 Ridpath, C. D. Haynes, and M. J. D. Williams.) pp. 125–131. (A.A. Balkema:
753 Rotterdam, Netherlands.)
- 754 Webb, G. J. W., Bayliss, P. G., and Manolis, S. C. (1989). Population research on crocodiles
755 in the Northern Territory, 1984-86. In ‘Crocodiles. Proceedings of the 8th Working
756 Meeting of the IUCN-SSC Crocodile Specialist Group’. pp. 22–59. (IUCN, Gland,
757 Switzerland.)
- 758 Webb, G. J. W., Britton, A. R. C., Manolis, S. C., Ottley, B., and Stirrat, S. (2000). The
759 recovery of *Crocodylus porosus* in the Northern Territory of Australia: 1971-1998. In

- 760 'Crocodiles. Proceedings of the 15th Working Meeting of the IUCN-SSC Crocodile
761 Specialist Group'. pp. 195–234. (IUCN, Gland, Switzerland.)
- 762 Webb, G. J. W., and Manolis, S. C. (1993). Conserving Australia's crocodiles through
763 commercial incentives. In 'Herpetology in Australia, A Diverse Discipline'. (Eds L.
764 Lunney and D. Ayers.) pp. 250–256. (Surrey Beatty & Sons: Sydney, Australia.)
- 765 Webb, G. J. W., and Manolis, S. C. (1992). Monitoring saltwater crocodiles (*Crocodylus*
766 *porosus*) in the Northern Territory of Australia. In 'Wildlife 2001: Populations'. (Eds
767 D. R. McCullough and H. D. Barrett.) pp. 404–418. (Elsevier Applied Science: New
768 York, USA.)
- 769 Webb, G. J. W., Manolis, S. C., and Brien, M. L. (2010). Saltwater Crocodile *Crocodylus*
770 *porosus*. In 'Crocodiles Status Survey and Conservation Action Plan'. (Eds S. C.
771 Manolis and C. Stevenson.) pp. 99–113. (Crocodile Specialist Group: Darwin,
772 Australia.) Available at:
773 http://www.iucncsg.org/365_docs/attachments/protarea/18%20--8088e67a.pdf
- 774 Webb, G. J. W., Manolis, S. C., Buckworth, R., and Sack, G. C. (1983). An Examination of
775 *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an
776 analysis of embryo mortality. *Wildlife Research* **10**, 571–605. doi:10.1071/wr9830571
- 777 Webb, G. J. W., and Messel, H. (1978a). Morphometric analysis of *Crocodylus porosus* from
778 the north coast of Arnhem Land, northern Australia. *Australian Journal of Zoology*
779 **26**, 1–27.
- 780 Webb, G. J. W., and Messel, H. (1979). Wariness in *Crocodylus porosus* (Reptilia:
781 Crocodylidae). *Wildlife Research* **6**, 227–234.
- 782 Webb, G. J. W., Messel, H., Crawford, J., and Yerbury, M. J. (1978). Growth rates of
783 *Crocodylus porosus* (Reptilia: Crocodylia) From Arnhem Land, northern Australia.
784 *Wildlife Research* **5**, 385–399.
- 785 Webb, G. J. W., Messel, H., and Magnusson, W. E. (1977). The nesting biology of
786 *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* **1977**, 238–249.
- 787 Webb, G., and Manolis, S. C. (1989). 'Crocodiles of Australia'. (Reed Books: Sydney,
788 Australia.)
- 789 Webb, G., Manolis, S., Whitehead, P., and Letts, G. (1984). 'A Proposal for the Transfer of
790 the Australian Population of *Crocodylus porosus* Schneider (1801), from Appendix I
791 to Appendix II of C.I.T.E.S.' (Conservation Commission of the Northern Territory:
792 Darwin, Australia.)
- 793 Webb, G., and Messel, H. (1978b). Movement and dispersal patterns of *Crocodylus porosus*
794 in some rivers of Arnhem Land, northern Australia. *Wildlife Research* **5**, 263–283.
- 795 Weber, W., and Rabinowitz, A. (1996). A global perspective on large carnivore conservation.
796 *Conservation Biology* **10**, 1046–1054. doi:10.1046/j.1523-1739.1996.10041046.x

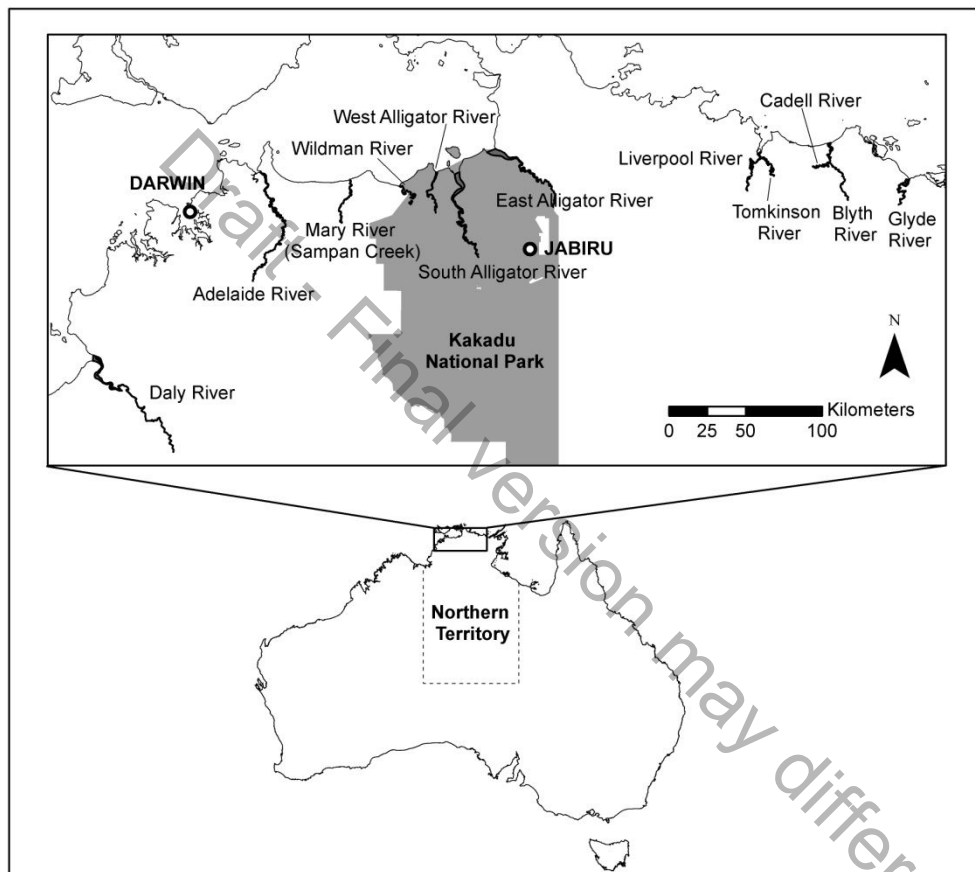
797 Wildlife Management International Pty. Limited [WMI] (2007). Monitoring Saltwater
 798 Crocodile (*Crocodylus porosus*) Nests in the Northern Territory: Trends in Melacca
 799 Swamp over 28 Years (1980-2007).

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801 **Conflicts of interest**

802 The authors declare no conflicts of interest.

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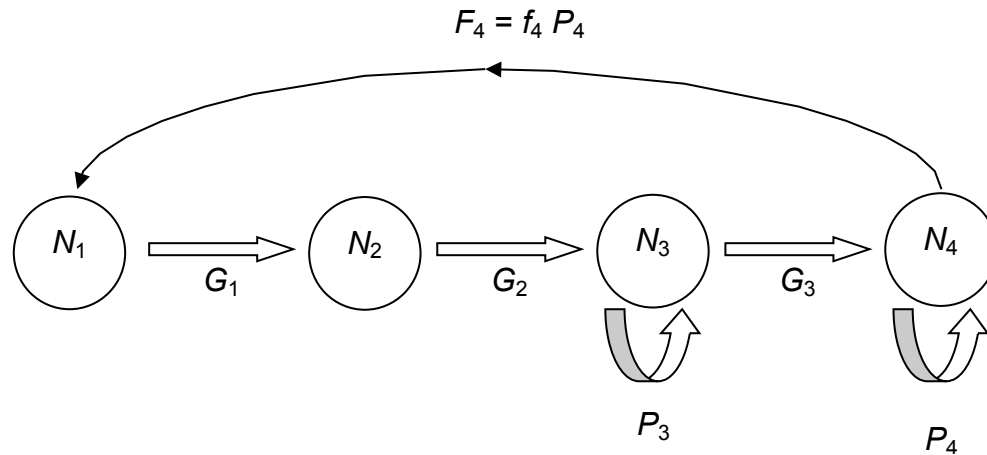


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805 **Figure 1.** Location of the study area, the Northern Territory of Australia showing the 12

806 rivers for which survey data were available.

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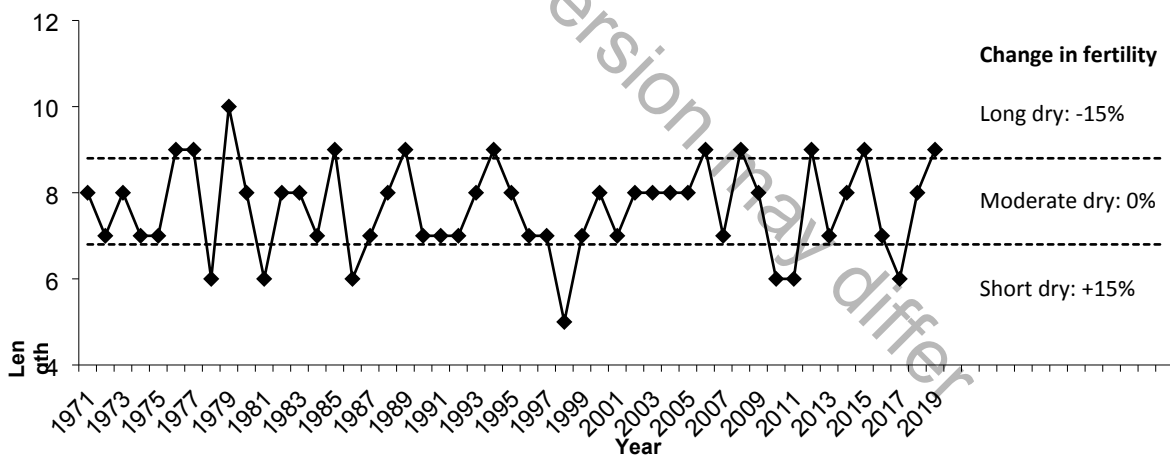


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809 **Figure 2.** Life cycle graph for *C. porosus* with post-breeding census representation.

810 N_1 = eggs, N_2 = hatchlings (>0.6 m TL), N_3 = juveniles (0.6-2.1 m TL), and N_4 = adults (>2.1
 811 m TL). P = persistence rate, G = transition rate, f = fertility, and F = reproduction. Note that
 812 there is not $G_3 F_4$ contribution to N_1 , because females in their first year of N_4 (2.1-2.3 m) are
 813 not sexually matured.

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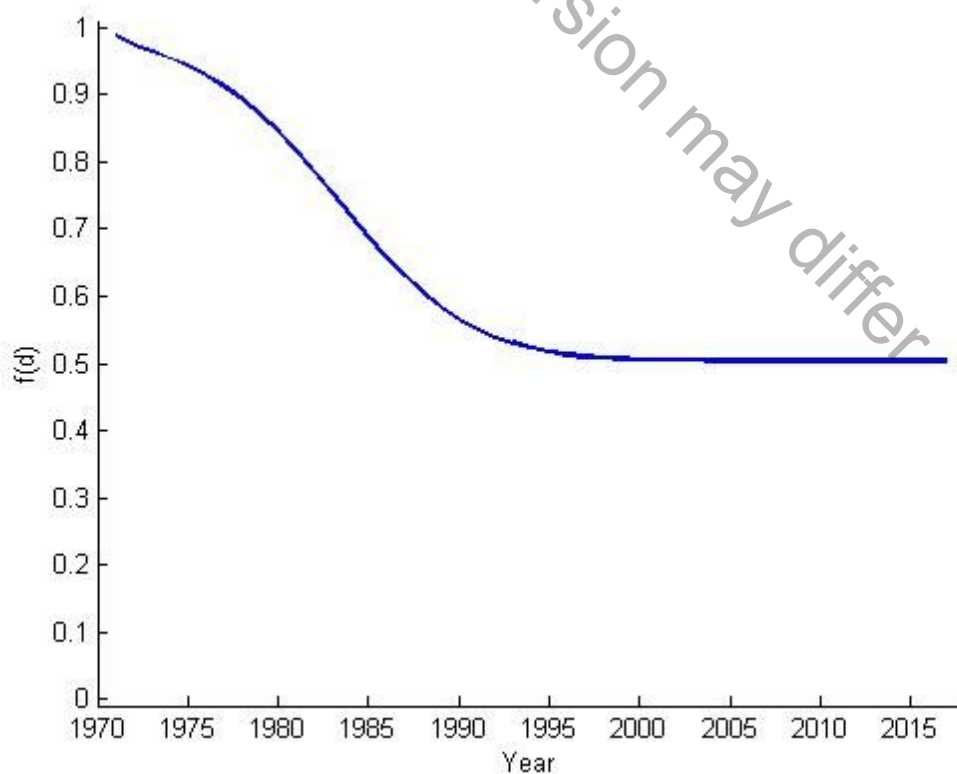
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816 **Figure 3.** Length of dry season at Darwin, Northern Territory of Australia between 1971 and
 817 2019. The length of dry season is the number of months from the last month with >100 mm
 818 rainfall in the previous wet season to the first month with >100 mm rainfall in the following
 819 wet season (data derived from the Darwin Airport, station number 14015, Bureau of
 820 Meteorology 2020). Reproduction (F) was assumed to decrease by 15% in the long dry
 821 season (≥9 months) and increase by 15% in the short dry season (<7 months).

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$$\begin{matrix} 823 \\ 824 \\ 825 \\ 826 \\ 827 \\ 828 \\ 829 \\ 830 \\ 831 \\ 832 \\ 833 \\ 834 \\ 835 \end{matrix}
 \begin{pmatrix} E_{t+1} \\ H_{t+1} \\ J_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & m_4 [\sigma_4(0) \exp(-\beta_4 A_t / h)] [f(0) / (1 + \beta_5 a_t / h)] \\ G_1 & 0 & 0 & 0 \\ 0 & \sigma_2(0) \exp(-\beta_2 H_t / h) & \{\sigma_3(0) \exp[-\beta_3 (J_t + A_t) / h]\} (1 - \gamma_3) & 0 \\ 0 & 0 & \{\sigma_3(0) \exp[-\beta_3 (J_t + A_t) / h]\} \gamma_3 & \sigma_4(0) \exp(-\beta_4 A_t / h) \end{pmatrix} \begin{pmatrix} E_t \\ H_t \\ J_t \\ A_t \end{pmatrix}$$

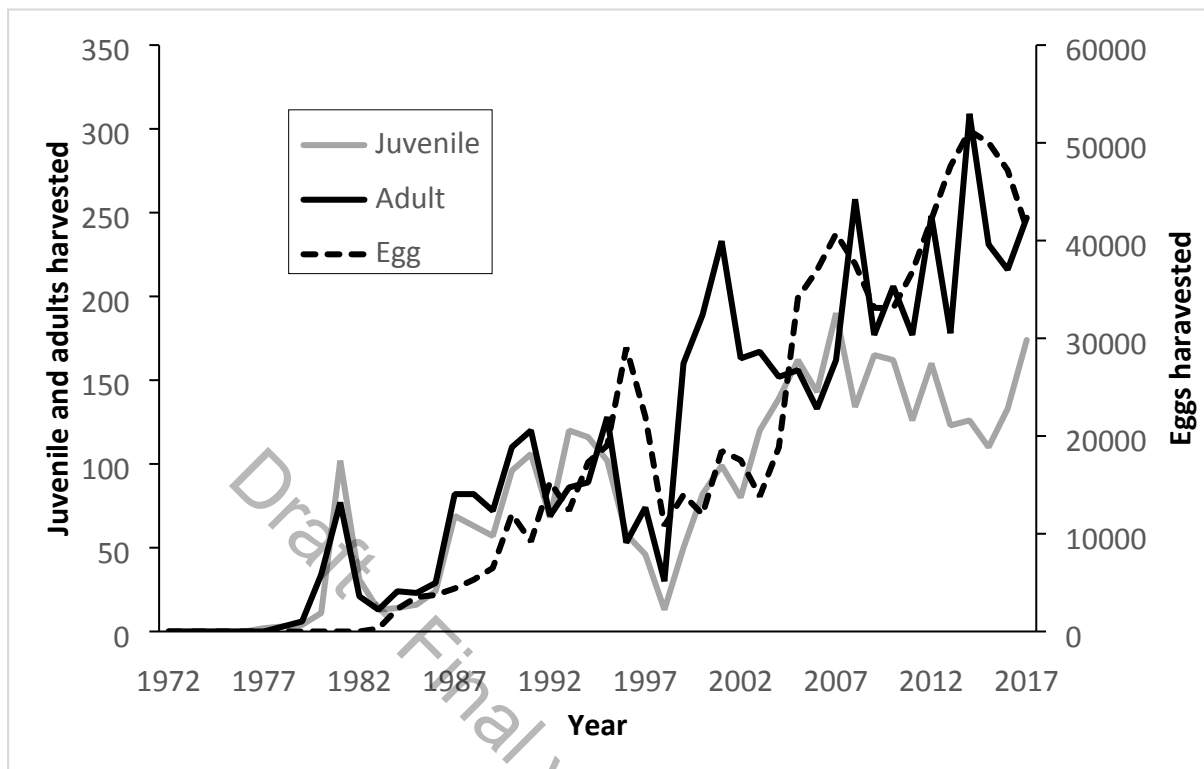
824 **Figure 4.** Stage-based matrix models for *C. porosus* with density dependence incorporated in
 825 survival (σ_i) and fertility (f). E_t , H_t , J_t , and A_t are the number of eggs, hatchlings (N_2),
 826 juveniles (N_3), and adults (N_4) at time t , respectively. a_t is the number of adult females at time
 827 t (total number of adults divided by sex ratio). β_2 , β_3 , and β_4 are measures of the strengths
 828 of density dependence in the survival of N_2 , N_3 , and N_4 , respectively. β_5 is the strength of
 829 density dependence in fertility. h is the total area of core habitats in the study area (18,843
 830 km²), derived from topographic analysis (Webb *et al.* 1984; Fukuda *et al.* 2007; Fukuda and
 831 Cuff 2013). γ_3 is the reciprocal of the duration of crocodiles in N_3 (see Table 1). m_4 is the
 832 number of female births in eggs per breeding female in N_2 per year. These matrices simulate
 833 demographic processes at each time step (= year) as a single population, combining males
 834 and females.



836 **Figure 5.** Proportions of females that breed every year in sexually matured (>2.3 m) females
 837 ($f(d)$) simulated by the stage-based matrix models with β_5 set at 0.45 for *C. porosus*.
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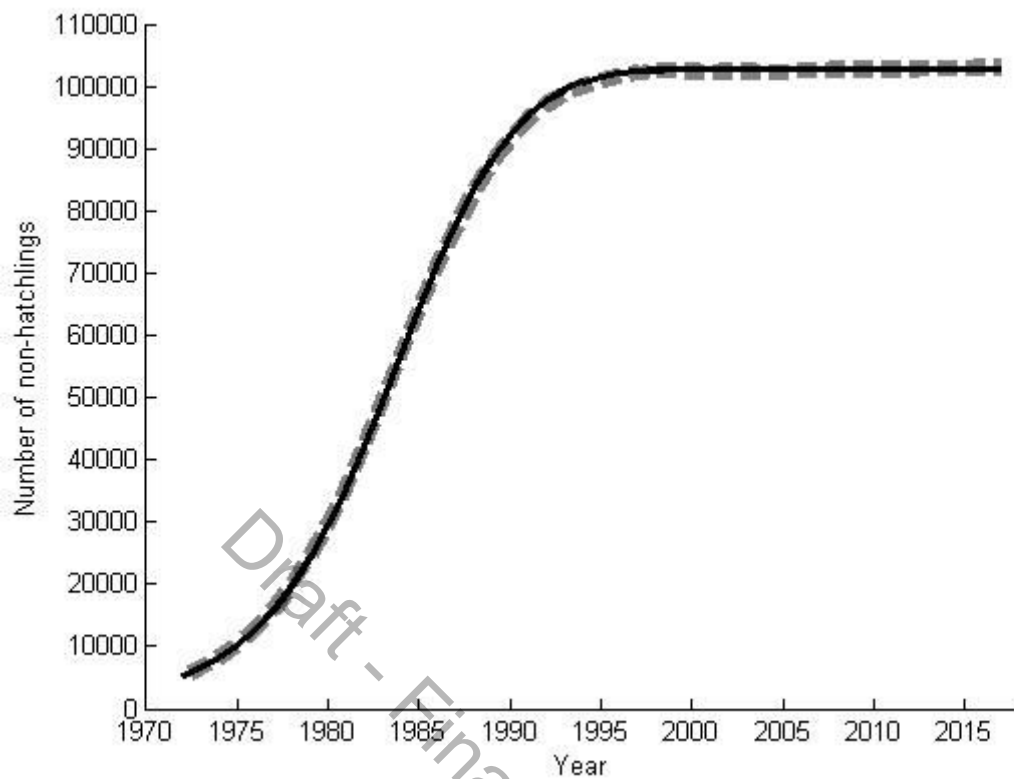
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Figure 6. Annual harvest of *C. porosus* in the Northern Territory of Australia for 1983-2017 (eggs) and 1977-2017 (juveniles (0.6-2.1 m TL) and adults (>2.1 m TL)).

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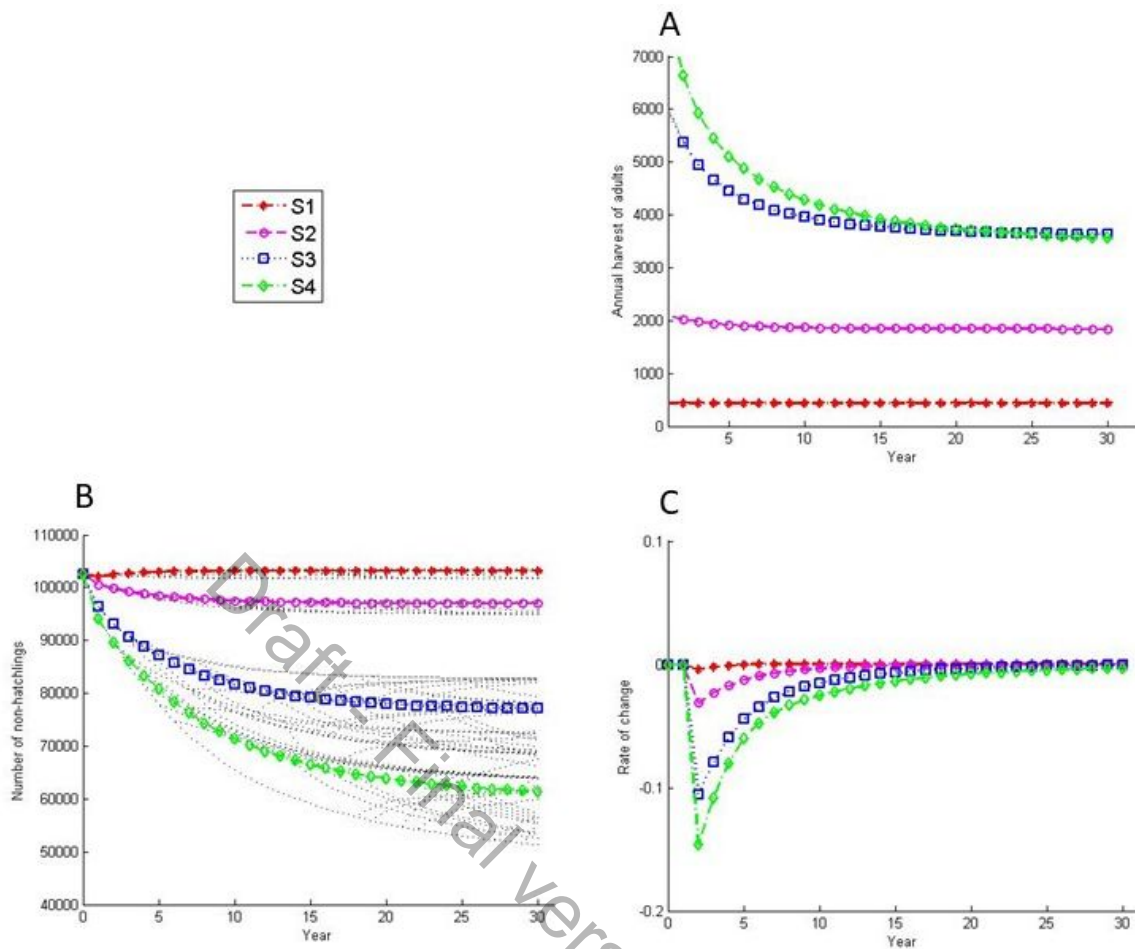
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847 **Figure 7.** The number of *C. porosus* non-hatchlings ($N_3 + N_4$) in 1971-2017 simulated by the
 848 stochastic, density-dependent models, with (broken line) and without (solid line) the actual
 849 harvest of eggs (1983-2017) and juvenile and adult crocodiles (1997-2017). Plotted lines are
 850 the mean of 500 iterations of each model.

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854
 855 **Figure 8.** The simulation of the different harvest scenarios (S1-S4) for *C. porosus* over 30
 856 years (2018-2047) by the stochastic, density-dependent models. Different levels of the
 857 harvest of crocodiles in N_4 (>2.1 m TL) were set for S1-S4 (A) while the harvest of N_1 was
 858 assumed constant at 20% of the simulated number of eggs (see text). The effects of the
 859 harvest under each scenario are shown in the number of non-hatchlings ($N_3 + N_4$, B) and the
 860 rate of change in crocodiles in N_4 (C).

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871 **Table 1.** Vital rates and matrix elements of *C. porosus* at each life stage.

872 See text for explanation for each variable. These vital rates were considered accurate at the
873 time of protection (1971). The effects of density-dependence and harvest on the vital rates
874 were incorporated in the model simulations (see text).

Stage	Vital rates			Matrix elements		
	σ_i	γ_i	m	G	P	F
N_1	0.25	1	-	0.25	-	-
N_2	0.54	1	-	0.54	-	-
N_3	0.72	0.12	-	0.09	0.63	-
N_4	0.97	0	26.50	-	0.97	25.70

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877 **Table 2.** Right (w_1) eigenvector and initial population vector (w_0).

878 w_1 and w_0 represent the proportion and the number of individuals in each life stage ($N_1 - N_4$)
879 at the time of protection (1971), respectively.

Stage	w_1	w_0
N_1	71.26%	19171.9
N_2	13.88%	3733.5
N_3	11.31%	3044.3
N_4	3.55%	955.7

880

881 **Table 3.** Density-dependence parameters estimated by fitting the density of *C. porosus* stages
882 (i) from spotlight surveys to a linear regression against the observed retention as defined by
883 Webb and Manolis (1992).

884 β_2 , β_3 and β_4 are the density dependence parameters of hatchlings (N_2), juveniles (N_3) and
885 adults (N_4), respectively. The standard error (SE) was calculated as the square root of the
886 mean squared deviation of the observed retention rates from the fitted line.

	β_2	β_3	β_4
Estimates	0.153	0.006	0.044
SE	0.002	0.006	0.003
P	<0.001	0.341	<0.001
Adjusted r^2	>0.999	<0.001	0.931

887

888 **Table 4.** Population size and structure of *C. porosus* simulated 46 years after protection
 889 (2017) with and without the harvests of eggs (N_1), juveniles (N_3), adults (N_4), and non-
 890 hatchlings ($N_3 + N_4$).

891 There was no harvest in hatchlings (N_2). The number is the mean of the 500 iterations \pm the
 892 standard error of the mean. The percentage of each stage in the total population is also shown.
 893 The total is of all the stages combined. Values are not definitive as the simulation involved
 894 random stochasticity in each iteration.

Stage	Not harvested	Harvested
N_1	682433.07 \pm 2615.89 (71.47%)	677516.93 \pm 2438.85 (72.14%)
N_2	170611.15 \pm 654.27 (17.87%)	159115.82 \pm 608.89 (16.94%)
N_3	57698.55 \pm 79.16 (6.04%)	58974.36 \pm 58.86 (6.28%)
N_4	44064.82 \pm 34.29 (4.62%)	43540.30 \pm 26.72 (4.64%)
$N_3 + N_4$	101763.37 \pm 113.26 (10.66%)	102514.66 \pm 85.49 (10.92%)
Total	954807.59 \pm 3159.09 (100%)	939147.41 \pm 2965.06 (100%)

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