Modelling effects of water regulation on the population viability of threatened amphibians

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Abstract

1. The regulation of river systems alters hydrodynamics and often reduces lateral connectivity between river channels and floodplains. For taxa such as frogs that rely on floodplain wetlands to complete their lifecycle, decreasing inundation frequency can reduce recruitment and increase the probability of local extinction.

2. We virtually reconstructed the inundation patterns of wetlands under natural and regulated flow conditions and built stochastic population models to quantify the probability of local extinction under different inundation scenarios. Specifically, we explored the interplay of inundation frequency, habitat size, and successive dry years on the local extinction probability of the threatened southern bell frog *Litoria raniformis* in the Murray River floodplains of South Australia. We hypothesised that the changes in wetland inundation resulting from river regulation are driving the decline of *L. raniformis* in this system.

3. Since river regulation began in the 1920s, the inundation frequency of many reliable breeding habitats has decreased to a point where they no longer support local populations. Increasing successive dry years drives the probability of local extinction, particularly in smaller wetlands. Larger wetlands and those with more frequent average inundation are less susceptible to these effects.

4. *Synthesis and Applications.* Although the availability of suitable habitats has reduced, environmental water provision is a promising tool to mitigate the negative impacts of river regulation on amphibian populations. Our modelling approach can be used to prioritise the delivery of environmental water (through pumping or the operation of flow-regulating structures) to minimise the probability of local extinction in *L. raniformis* and potentially many other frog species. By quantifying the extinction risk of amphibian populations, we can strategically manage environmental water to reduce successive catastrophic breeding failures and increase the probability of persistence.

Introduction

The global decline of amphibians (Blaustein & Wake 1990; Stuart *et al.* 2004) is stark, with the most recent figures showing 41% of assessed species are threatened with extinction (IUCN 2020). Furthermore, extinctions and declines are projected to increase through the 21st Century as the interactive drivers of extinction increase in intensity (Hof *et al.* 2011). Human modifications of wetland networks via river regulation can reduce lateral connectivity and the ecological function of wetland habitats (Castello & Macedo 2016) that are essential breeding and nursery areas for many amphibian species. This can change amphibian community structure and cause local extinctions (Wassens & Maher 2011).

The negative consequences of river regulation on amphibians are predicted to increase as climate change progressively overtakes land use (Narins & Meenderink 2014) as the main driver of amphibian richness patterns and species loss (Newbold 2018). Aridification due to climate change can reduce the availability of breeding habitats resulting in reduced species richness (McMenamin, Hadly & Wright 2008), and the combination of aridification and increasing water consumption are likely to reduce the availability of freshwater habitats further in some regions (Miller *et al.* 2018).

Manipulating water resources can help alleviate the effects of declining water availability and support amphibian recruitment (Shoo *et al.* 2011; Smith, Meredith & Sutherland 2019; Mathwin *et al.* 2020). Techniques for manipulating water to benefit amphibians vary in their approach and success (Mathwin *et al.* 2020), but the best-supported approach is the provision of water to breeding habitats to match the larval requirements of the target species ('environmental water provision'). This is because enhancing survival through breeding and early life stages can stabilise populations (Griffiths & Pavajeau 2008). The targeted delivery of environmental water is a common practice today (Kennen, Stein & Webb 2018) and could become necessary to conserve some species (Greenwood *et al.* 2016),

82   especially those with limited phenotypic plasticity or those near the edge of their ecological

83   niche (Grant, Miller & Muths 2020).

84   Australia's Murray-Darling Basin provides a model system to examine this process.

85   The catchment is heavily regulated and up to 61% of total flow is extracted for consumptive

86   use (CSIRO 2008). This has reduced the number and function of wetlands (Gell & Reid

87   2014), resulting in the decline of water-dependent taxa (including the southern bell frog,

88   *Litoria raniformis*) (Clemann & Gillespie 2012). In response to systemic environmental

89   degradation, federal legislation mandates interventions aimed at restoring ecological function

90   (Docker & Robinson 2014), including environmental water provision for species recovery.

91   In this paper, we explore hydro-ecological thresholds and generate guidelines for

92   environmental water provision to benefit amphibians by constructing stochastic, hydro-

93   ecological population models. We hypothesise that the reduced frequency of wetland

94   inundation resulting from river regulation is driving local extinction events of *L. raniformis* in

95   the Murray River of South Australia. We hypothesise that larger wetlands and wetlands with

96   higher average inundation are less susceptible to local extinction during successive dry years.

97   We posit that the probability of local extinction can be reduced by environmental water

98   provisions that decrease the number of successive years without recruitment. Based on these

99   results, we argue that stochastic population models provide a sound approach for quantifying

100   local extinction risk and hence, triaging environmental water provision to at-risk populations.

101

Materials and Methods

103   *Study area*

104   The Murray-Darling Basin contains Australia's longest river system and is heavily regulated

105   to provide water for domestic and agricultural use. Regulating structures include a series of

106   14 main-channel weirs ('locks') that dissect the river. Our focus is 70 km of the Murray River

107   channel between Lock 3 (34° 11′ 16.95″ S, 140° 21′ 29.65″ E) and Lock 2 (34° 4′ 39.31″ S,

108   139° 55′ 52.81″ E) and the associated wetlands and floodplains along this reach (**Figure 1**).

109   This region receives an annual rainfall between 160 and 240 mm (semi-arid/arid), which is

110   insufficient to fill off-channel wetlands most years. As such, all naturally occurring wetland

111   inundation results from elevated river level.

112
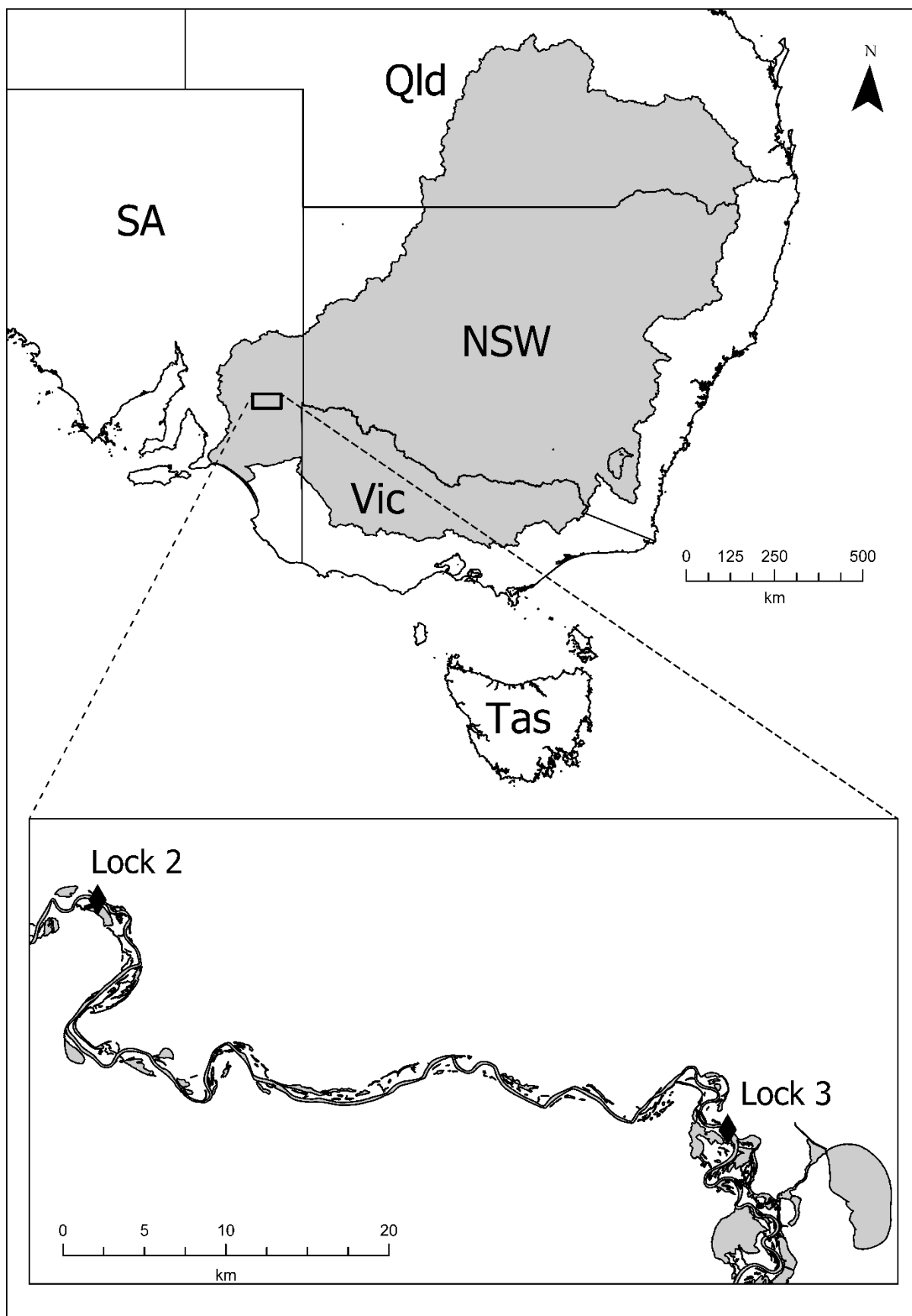
Figure 1 The reach between Locks 3 and 2 is at the downstream end of the Murray-Darling catchment (shaded grey). Flow is strongly influenced by regulation and extraction throughout

115 the upstream reaches. Australian states are: SA= South Australia, Qld = Queensland, NSW =
116 New South Wales, Vic = Victoria and Tas = Tasmania.

117

118 *Life history of southern bell frogs*

119 There are many experimentally derived data describing the life history of *L. raniformis*, with

120 relationships established for most vital rates (survival, growth, reproduction, and

121 recruitment). Eggs hatch two to four days after laying (Anstis 2002). The likelihood of hatch

122 (as a proxy for egg survival rate) is between 0.933 and 1.000. This species ranges from north

123 of latitude 35 °S to south of 45 °S, which spans a range of thermal conditions (from 32.9 °C

124 maximum daily summer temperatures in the north of their range to 20.5 °C in the south).

125 Being ectotherms, larval duration is strongly driven by temperature and as such, larval

126 duration varies from 10–12 weeks in the north of their range to 12–15 months in the south

127 (Anstis 2002). We used the larval duration of 70–80 days calculated at a constant water

128 temperature of 23 °C (Cree 1984), approximately the average daily summer temperatures

129 experienced in the study reach (which averages diurnal highs and nocturnal lows). We used

130 the estimates of survival to metamorphosis generated for *Crinia signifera* (15–26% and 7–

131 56%) (Williamson & Bull 1999), in the absence of species-specific estimates, these are the

132 most-relevant estimates available.

133   Both sexes reach maturity in their first year (Heard, Scroggie & Malone 2012) and

134 females breed annually (Anstis 2017) laying between 1885 and 3893 eggs each season

135 (Humphries 1979). We used annual adult survival probability from the closely related *Litoria*

136 *aurea* (mean = 0.2172, standard deviation = 0.087) (Pickett *et al.* 2016). These species are

137 similar in size, appearance, and behaviour, although *L. aurea* occurs along a more northerly

138 latitude than *L. raniformis*. Using lines of arrested growth in the shaft of the medial phalanx

139 to determine age (skeletochronology), *L. raniformis* can survive into their fifth year (Mann *et*

140 *al.* 2010) (G. Heard and A. Turner, Charles Sturt University, pers comm.).

141

Demographic model
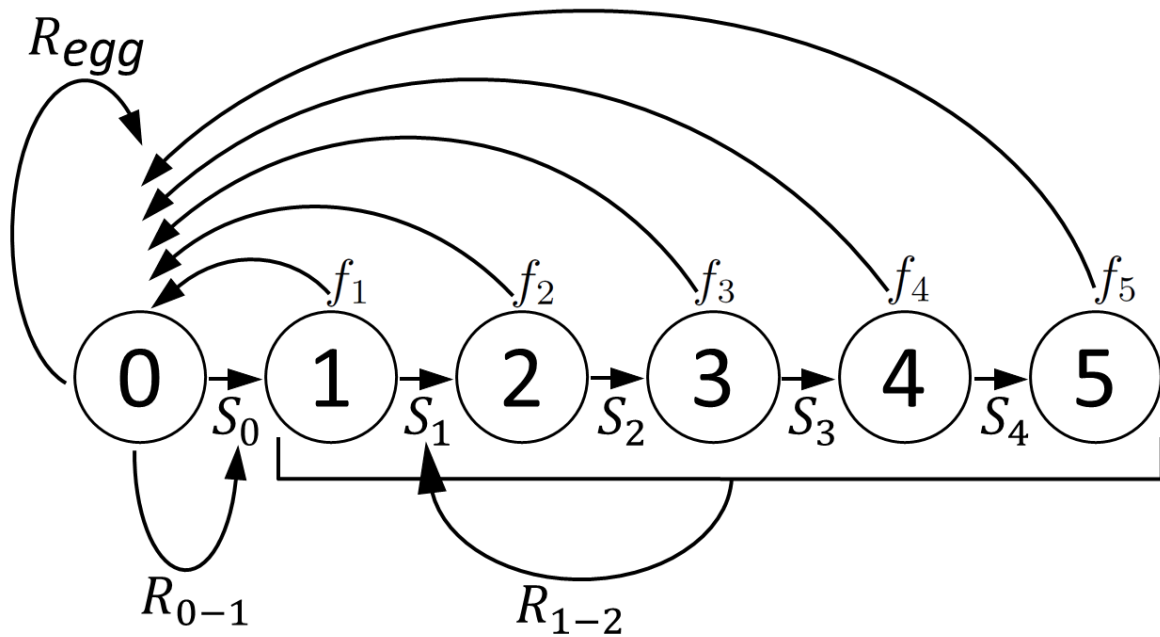
Figure 2 *Litoria raniformis* can live into the fifth year. Compensatory density-feedback reduction (*R*) in annual survival probability (*S*) and fertility (*f*) are calculated from both population and wetland size.

We constructed the model based on a lifecycle graph (**Figure 2**) and an age-classified (Leslie) population model (Leslie 1945) that considers only females (**Figure S1**), where *f* represents fertility and *S* represents annual survival. Year 0 individuals do not breed and are not assigned a fertility. We randomly resampled fertilities (*f*) for age classes one to five years from a normal distribution between 1885 and 3893 eggs (Humphries 1979), which we halved to reflect the 50:50 sex ratio in this species.

We calculated survival *S* to the end of the first year as:

$$S_0 = S_e * S_t * ((365 - (D_e + D_t)) * S_{ad}) \qquad \text{[equation 2]}$$

where S_0 is the probability of survival from 0 to 1 year old. S_e is the probability of hatch (randomly resampled from a uniform distribution from 0.933–1.000). S_t is the probability of

158   survival to metamorphosis, which we randomly resampled from a β distribution with a mean

159   = 0.26 and a standard deviation = 0.12 (Williamson and Bull 1999). We calculated the shape

160   parameters α and β of this distribution using:

161
$$\alpha \; = \; m \frac{\mu(1-\mu)}{\sigma^2}$$
[equation 3]

162
$$\beta = (1 - \mu)\left(\frac{m\mu(1-m\mu)}{\sigma^2} - 1\right)$$
[equation 4]

163   where μ is the mean and σ is the standard deviation of the β distribution. D_e is the duration of

164   the egg stage (in days) resampled randomly from a uniform distribution between 2 and 4, and

165   D_t is the duration of the tadpole stage (in days) resampled randomly from a Normal

166   distribution between 70 and 80 days. S_{ad} is the daily adult survival probability calculated as:

167
$$S_{ad} \; = \; \sqrt[365]{S_a}$$
[equation 5]

168   where S_a is the annual probability of survival of an adult frog sampled from a β distribution

169   with a mean = 0.2172 and a standard deviation = 0.087 (Pickett *et al.* 2016). We assigned

170   frogs in their fifth year a survival = 0, reflecting senescence and death during their fifth year

171   (although the model permits breeding before death).

172

173   *Population sizes*

174   We modelled *L. raniformis* populations at each of four wetland sizes (*small*, *medium*, *large*,

175   *very large*). We derived these categories from typical wetlands in the region and the

176   corresponding population size is an estimate of their respective carrying capacity. *Small*

177   populations (~ 40 individuals) reflect the carrying capacity and population dynamics present

178   in a wetland pool several metres in diameter. A *medium* population (~ 130 individuals)

179   represents a wetland pool similar to 1–2 domestic swimming pools. A *large* population (~

180   300 individuals) represents a wetland pool similar to an Olympic swimming pool, and a *very*

181   *large* population (~ 1000 individuals) reflects a wetland several hundred metres in diameter.

182   The starting population of adult females was calculated as 50% of these values (as *L.*

183   *raniformis* has a 50:50 sex ratio), being 20, 65, 150 and 500 female frogs, respectively. We

184   assigned age classes for the starting female population by randomly resampling five adult

185   survival values and then dividing the total number of females among the five age classes in

186   these proportions. This created a more homogenous initial age structure than we might expect

187   in a wild population. We managed this by ignoring the first 10 generations of each run as a

188   'burn-in' period, which allowed the model to stabilise to a stochastic expression of the stable-

189   age distribution before analysis.

190   We allocated the initial number of eggs using an *a priori* number of spawning masses

191   for each wetland size ($n = 10, 30, 85, 150$, respectively). We then stochastically resampled

192   the number of eggs in each spawning mass (halved because the model only considers

193   females). At these densities the *a priori* assignment of spawning masses did not impact

194   population dynamics after burn-in.

195

196   *Compensatory density feedback*

197   To stabilise long-term population growth, we incorporated three compensatory density-

198   feedback relationships. First, we corrected rates of egg laying to reflect the maximum

199   carrying capacity (K_{egg}) at each wetland. As the number of eggs approaches the wetland's

200   carrying capacity, eggs are reduced following an exponential decay function of the form:

201    $$y = 1.01 - (x^{2+\frac{9}{x}})$$ [equation 6]

202   and the rate of egg reduction follows the equation:

203    $$R_{egg} = \int_0^{0.99} 1.01 - \left(K^{2+\frac{9}{K}}\right) d_K$$ [equation 7]

204   where R_{egg} is the total reduction in eggs laid at the wetland, K is the carrying capacity and d_K

205   is the differential K (carrying capacity) (**Figure S2**). Carrying capacity is calculated for each

206   wetland size category using the initial number of *a priori* spawning masses laid (10, 30, 85 or

207   150) at the maximum fecundity for the species (3893 eggs), which we halved to consider only

208   females. In this way, frogs lay without inhibition until the total egg count approaches the

209   carrying capacity. The highest inhibition rate corresponds to 0.99 of the wetland's carrying

210   capacity and all subsequent egg-laying events are reduced at this value (corresponding to a

211   reduction of 0.0078).

212   The second compensatory density-feedback function used the total number of tadpoles

213   present to reduce survival probabilities during the first year of life. This reflects predation and

214   competition during larval life stages, and in the first few months post-metamorphosis. We

215   calculated density feedback on survival probability using the function:

216                     $$R_{0-1} = (-0.241 + 1.54K))^{-0.855}$$ [equation 8]

217   where R_{0-1} is the reduction factor in survival for age class 0 individuals (**Figure S3**). Here,

218   we assigned carrying capacity *a priori* based on the size of the wetland, *small* = 200 females,

219   *medium* = 600 females, *large* = 1800 females and *very large* = 3000 females. Density

220   feedback on survival from 0- to 1-year age classes is applied when the total adult population

221   > 0.3 of the wetland's carrying capacity. We applied the highest reduction in survival at 2.1

222   times carrying capacity that reduces survival probability to 0.0101 (Figure S3).

223   The third compensatory density-feedback function applies the abundance of all adult

224   frogs to reduce survival from the 1- to 2-year age class (R_{1-2}) to reflect competition for

225   resources. The form of the relationship followed the method applied for (R_{0-1}) presented

226   above (equation 8, **Figure S3**).

227

228   *Modelling hydrology*

229   We considered two river-flow scenarios. The 'regulated flow' scenario is informed by the

230   historical flow record immediately downstream of Lock 3 (A4260517;

231   waterconnect.sa.gov.au). We used data starting in 1926, the year following the completion of

232   Lock 3. River levels above the operative range of this gauge 'drown out' the gauge, making

233   measurements inaccurate. During these periods, we used data from station A4260528 (6.5 km

234   downstream of Lock 3), which is unaffected by elevated river levels. This created a

235   continuous daily record of flow rate between Locks 3 and 2 for 83 years. The second river-

236   flow scenario is modelled 'natural flow', which covers the same time period, but in the

237   absence of extraction or regulation in the catchment (see Murray-Darling Basin Authority-

238   MDBA 2012a).

239   A second-order polynomial derives river heights from mean daily flow rate (Ml day^{-1})

240   for the two flow scenarios. Based on mean daily river height (metres with respect to

241   Australian River Height Datum, mAHD) at site A4260517 and the flow records above, the

242   following rating-curve equation:

243      $$H = -2f^2 10^{-10} + 8f 10^{-5} + 6.0144$$ [equation 9]

244   estimates river height, where H is river height (mAHD) and f is river flow (Ml day^{-1}). We

245   used this to create a continuous daily river height for this reach over 83 years under natural

246   and regulated flow.

247   Our model exposes wetland populations to one of two states each year. A 'wet' year is

248   when the wetland received sufficient water to support frog reproduction and recruitment;

249   conversely, during a 'dry' year, the wetland did not receive sufficient inputs to support frog

250   recruitment (often filling and then drying prematurely — see definition below). There is a

251   paucity of accurate sill-height (the river height at which a wetland begins to fill) data in the

252   reach, so rather than modelling the inundation of specific wetlands, we calculated inundation

253   of nine possible sill heights (7, 7.5, 8, 8.5, 9, 9.5, 10, 10.5 and 11 mAHD). Following

254   discussion with local wetland managers, we used the rule that if mean daily river height is $\geq$

255   10 cm above sill height for $\geq$ 10 days during winter and spring, then the wetland is 'wet' and

256   can support frog recruitment that year (K. Mason – Department for Environment and Water,

257   Adelaide, pers comm.). It is not necessary that these ten days be consecutive to fulfil this

258   criterion. By using this criterion, we determined which of the nine sill heights were wet, and

259   which were dry for each of the 83 years under the natural and regulated scenarios.

260

261   *Modelling flow scenarios*

262   We modelled 18 hydrological scenarios — these being sill heights of 7, 7.5, 8, 8.5, 9, 9.5, 10,

263   10.5 and 11 mAHD each modelled under both natural- and regulated-flow conditions. To

264   create stochastic expressions of these scenarios, we used the 83 years of daily river-height

265   data for the flow scenario (natural or regulated flow) and classified each of those 83 years as

266   either filling the nominated sill height ($\geq$ 10 non-consecutive days exceeding the sill height

267   by $\geq$ 10 cm during the previous winter or spring) to create a wet year, or failing to fill the sill

268   height sufficiently and creating a dry year (when recruitment is unsuccessful). Using this

269   sequence of 83 wet and dry years (for each specific sill height and flow combination) we

270   created a discrete-time Markov chain (e.g., Supporting Information 1) to resample unique,

271   stochastic, 85-year wet/dry sequences for each model scenario run.

272   Finally, we modelled each of the four wetland sizes (*small*, *medium*, *large*, *very large*)

273   at each of nine sill heights (7, 7.5, 8, 8.5, 9, 9.5, 10, 10.5 and 11 mAHD) and each of two

274   flow scenarios (natural and regulated flow). We ran each of these 72 wetland models

275   stochastically 10,000 times, each for 85 consecutive generations or until the population went

276   extinct (creating a combined total of 61.2 million stochastic generations). This was sufficient

277   to account for wetland variability in the study reach. We disregarded the first ten burn-in

278   generations of each model and used generations 11 to 85 (or to extinction) in our analyses.

279   For each model, we recorded the sequence of wet and dry years from generations 11 to

280   85 (or extinction). For each occurrence of two or more consecutive dry years, we recorded

281   the number of consecutive dry years and whether it resulted in extinction. We organised these

282   data by the average frequency of dry years at the wetland and calculated the probability of

283   extinction for two to five consecutive dry years, noting that six consecutive dry years exceeds

284   the maximum reproductive lifespan of the species.

285   To examine the effect of maximum lifespan on the model, we ran a univariate

286   sensitivity analysis on a single wetland model with senescence constrained to ages two, three,

287   four and five years (Supplementary Information 1).

288

Results
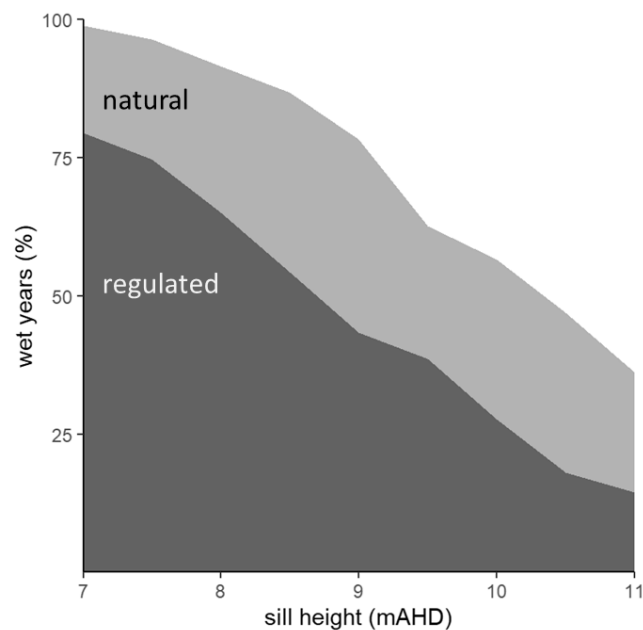
290

291   **Figure 3.** Proportion of the 83 years of observed river height (regulated) and modelled
292   natural river height that potentially supported *L. raniformis* breeding (wet years) at sill
293   heights from 7 to 11 mAHD.

294

295   *'Wetness' of wetlands under natural- and regulated-flow conditions*

296   River regulation reduced the frequency of wet years by 19–34% compared to the natural-flow

297   scenario for the same 83-year period (**Figure 3**). This equates to a reduction of wet years by

298   19.5% at 7 mAHD, up to 60% at 11 mAHD. This changed both the proportions and pattern of

299   wet and dry years. Regulation increased the mean duration of successive dry years at all sill

300   heights (**Figure 4**). Under natural conditions the mean duration of dry years did not exceed

301   two years at any of the sill heights examined, whereas the regulated-flow scenario resulted in

302   mean duration of dry events approaching the maximum lifespan of the species at sill heights

303   ≥ 10 mAHD. Under natural conditions the maximum duration of dry events did not exceed

304   the maximum reproductive lifespan of the species, except at a sill heights > 10 mAHD. The

305   maximum duration of dry events observed under river regulation exceeded the maximum

306   reproductive lifespan of this species at every sill height examined.
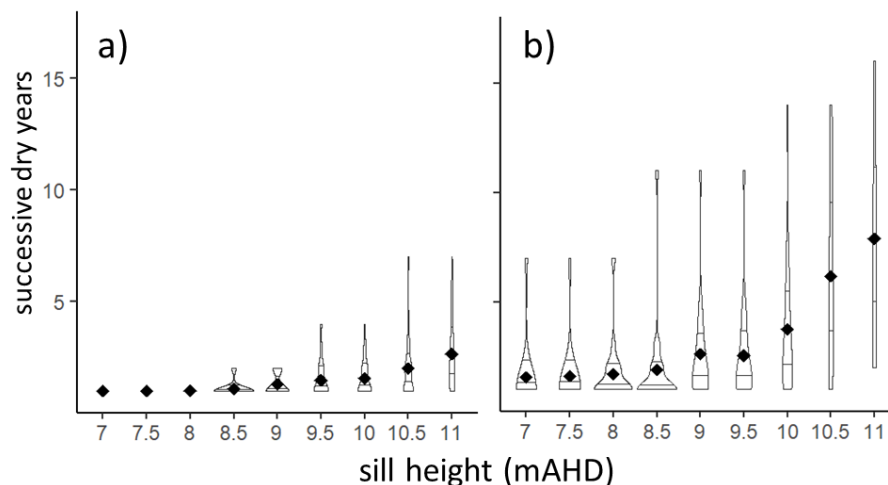
307

308   **Figure 4** Comparison of wetland inundation pattern over 83 years of observed data under a)
309   natural flow regime and b) river regulation. Sill heights are presented in metres with respect
310   to Australian River Height Datum (mAHD). The maximum duration of dry years exceeds the
311   maximum reproductive lifespan of *Litoria raniformis* under all regulated sill height wetlands.

312

Extinction probability of each wetland scenario

314   Under the natural-flow scenario, the probability of extinction — Pr(Ext) — during the 85

315   modelled years was ~ 0 at sill heights ≤ 8.5 mAHD (**Figure 5**). Conversely, all wetland sizes

316   reached Pr(Ext) = 1 at sill heights ≥ 9 mAHD when flows were regulated. Thus, wetlands that

317   historically supported *L. raniformis* populations under natural-flow conditions (i.e., ≤ 8.5

318   mAHD) are unreliable under river regulation. Without intervention, wetlands with sill height

319   of ≥ 9 mAHD will not sustain *L. raniformis* populations under existing flow conditions.

320   The probabilities of extinction in *very large* wetlands were 0.25 to 0.70 lower than

321   those in *small* wetlands (**Figure 6**). This effect was more pronounced in the regulated-flow

322   scenario than under natural-flow conditions.
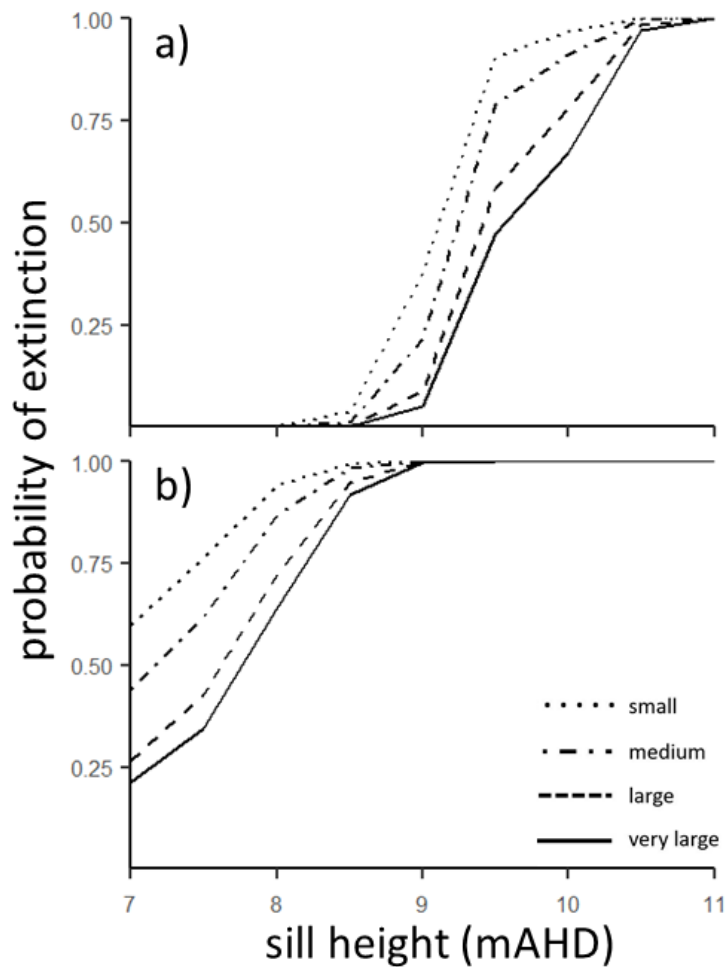
323

324   **Figure 5** The probability of extinction at four wetland sizes under a) natural-flow and b)
325   regulated-flow conditions. River regulation has increased the extinction probability of *Litoria*

326 *raniformis* populations through most of their former habitats. These effects are strongest at
327 smaller wetlands.

328

329
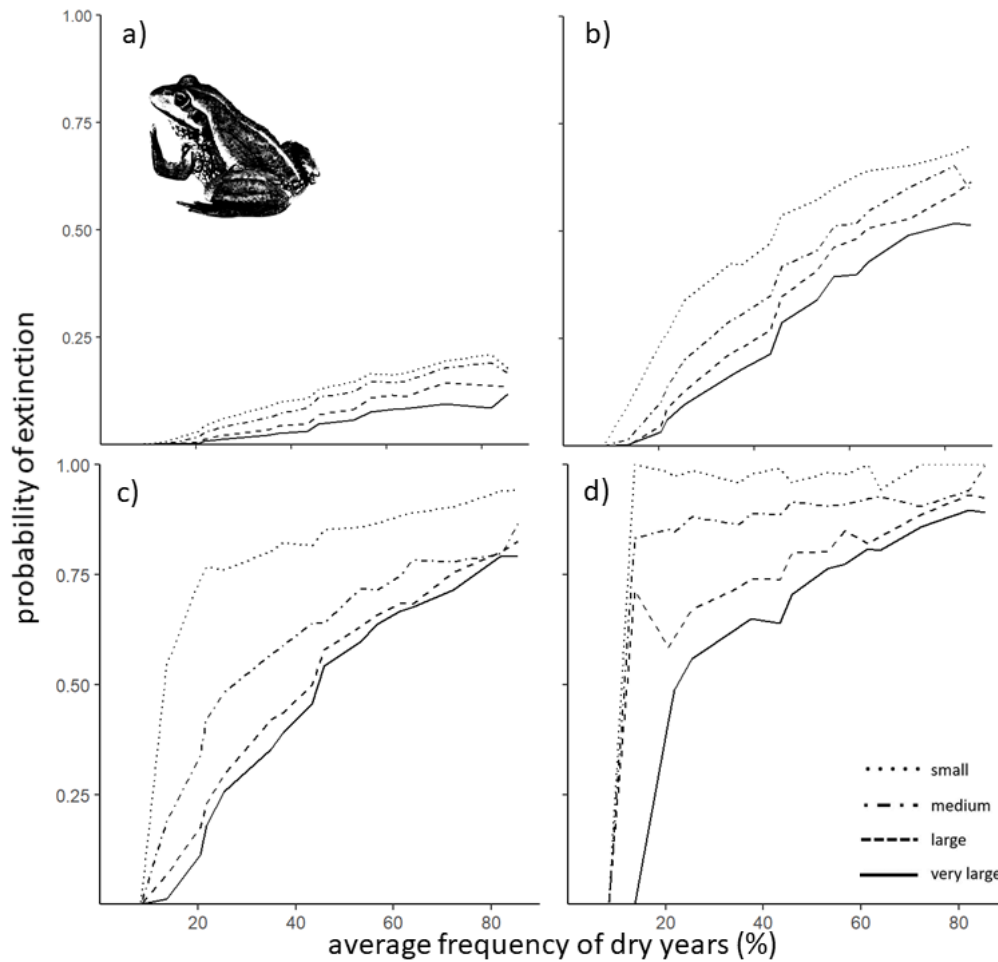
Figure 6 Successive dry years increase the probability of extinction and this effect increases
331 with: increasing dry duration, decreasing wetland size, and increased average frequency of
332 dry years at the wetland. Plots are a) 2 successive dry years, b) 3 successive dry years, c) 4
333 successive dry years and d) 5 successive dry years.

334

335 Two consecutive dry years resulted in Pr(Ext) < 0.25 in all treatments, including wetlands

336 with an 80% average frequency of dry years (**Figure 6**). Increasing the number of

337 consecutive dry years increases Pr(Ext) up to five consecutive dry years, which gives Pr(Ext)

338 > 0.5 in all treatments except for *very large* populations with an average frequency of dry

339 years < 20%. Smaller wetlands had increased extinction probability in all instances and the

340   disparity between wetland sizes became more pronounced with increasing successive dry

341   years. The average frequency of dry years at the wetland strongly influences the capacity to

342   survive extended dry periods. Wetter sites have lower extinction probability than drier sites

343   for each drought duration.

344

345   **Discussion**

346   Regulation and abstraction of flow in the Murray-Darling catchment has resulted in wetlands

347   that fill less often (**Figure 3**). The average duration of successive dry years has increased by

348   up to three years compared to natural flow conditions (**Figure 4**) (Maheshwari, Walker &

349   McMahon 1995; Bice *et al.* 2017). For species that rely on floodplain inundation to complete

350   their lifecycle, dry years result in reproductive failure. This is not uncommon in amphibians,

351   especially in species that breed in ephemeral waterbodies (which can dry before completion

352   of larval life stages). In isolation, reproductive failure causes population fluctuation, but do

353   not always appreciably increase the probability of local extinction (Taylor, Scott & Gibbons

354   2006), albeit with simplification of age structure and attrition of adult populations. However,

355   successive failures increase extinction risk, especially in short-lived species (Semlitsch *et al.*

356   1996). Without the capacity to extend lifespan through unfavourable periods (i.e.,

357   aestivation), droughts equalling or exceeding the reproductive lifespan of a species result in

358   local extinction, a process that is likely to have driven the local extinctions in 42% of

359   breeding sites of *Pseudophryne pengilleyi* in Kosciuszko and Brindabella National Parks in

360   New South Wales, Australia (Scheele *et al.* 2012).

361

362   *Drought and the decline of* Litoria raniformis

363   The flow record that informs our model includes a severe drought from 1996 to 2009. During

364   this time, south-eastern Australia experienced a region-wide reduction in rainfall and runoff,

365 below-average streamflow, and critical water shortages (Heberger 2011; van Dijk *et al.*

366 2013). This event, coupled with ongoing water extraction, resulted in seven or more

367 successive dry years at all sill heights ≥ 7 mAHD in this reach (**Figure 4**). The persistence of

368 some few *L. raniformis* through this period is probably a combination of breeding in the river

369 channel, the maintenance of some wetlands with environmental water, and recolonisation

370 with the return of flow in 2010 (Fonte, Mayer & Lötters 2019). The drought devastated *L.*

371 *raniformis* populations in the reach, but modelled natural flow for the same period indicates

372 that the maximum number of successive dry years would not have exceeded four years in

373 wetlands up to 10 mAHD (**Figure 4**). For *L. raniformis* that can breed in its fifth year, all

374 wetlands < 10 mAHD could have survived this perturbation.

375   *Litoria raniformis* was common throughout south-eastern Australia (Pyke 2002), but is

376 declining across its range (Osborne, Littlejohn & Thomson 1996; Ashworth 1998; Wassens *et*

377 *al.* 2010, Mason 2013). Proposed threatening processes are habitat loss, barriers to

378 movement, disease, predation by exotic fishes, biocides, and increases in ultraviolet B

379 radiation (Clemann & Gillespie 2012). Our results support our hypothesis that reduced

380 wetland inundation is driving population decline in this reach. Although this is reach-specific,

381 similar reductions in inundation are present elsewhere in the catchment and in other

382 catchments with declining *L. raniformis* populations. The link between river regulation and

383 increased extinction probability could be applicable at wetlands outside of this reach.

384

385 *Model assumptions*

386 Our model makes two main assumptions: that *L. raniformis* breed in their fifth year before

387 senescence, and there is no population exchange between wetlands. Our single-parameter

388 perturbation (sensitivity) analysis of maximum age (**Supplementary Information 1**) shows

389 little influence of maximum age on extinction probability. This is likely because the

390   demography of this species favours younger age classes. Reducing the maximum age of the

391   species does, however, reduce the maximum drought length before local extinction. If the

392   lifespan of *L. raniformis* in this system is lower than five years, then our outputs can be used

393   to triage environmental water provision to minimise the probability of local extinction.

394   However, when successive breeding failures meet the local maximum age, the population

395   will be lost regardless.

396   The second potential limitation of the model is that virtual wetlands exist in isolation

397   without immigration or emigration. As such, modelled local extinctions are an endpoint after

398   which recolonisation cannot occur. Amphibians are physiologically dependent on moist

399   environments, have relatively poor dispersal capacity (compared to other tetrapods), and can

400   show strong site fidelity, and these traits suggest limited capacity for recolonisation

401   (Blaustein, Wake & Sousa 1994). Despite limited dispersal, amphibians are frequently

402   thought to exist in metapopulations (Levins 1969; Smith & Green 2005). We propose that *L.*

403   *raniformis* in this system meets the four characteristics of a metapopulation (Hanski *et al.*

404   1995): (*i*) habitat patches support local breeding populations, (*ii*) no single population is large

405   enough to ensure long-term survival, (*iii*) patches are not too isolated to prevent

406   recolonisation, and (*iv*) local dynamics are sufficiently asynchronous to make simultaneous

407   extinction of all local populations unlikely. Despite the semi-arid/arid climate, *L. raniformis*

408   can move hundreds of metres in a single night and can colonise over distances of 500 m

409   (Herbert 2000; Department for Environment and Heritage, 2004; Wassens et al. 2008). We

410   anticipate that movement between favourable patches is critical to the persistence of this

411   species.

412   Nevertheless, our model informs the conservation of fragmented amphibian populations

413   with high resistance to dispersal. As a cautionary approach, our model considers the

414   population dynamics of isolated wetlands given that these have higher extinction probabilities

415   than wetlands within in a network. We anticipate that populations in close proximity will

416   have lower extinction probabilities than we predict here due to the stabilising effects of

417   metapopulation structure and the rescue effect (Brown & Kodric-Brown, 1977), but we urge

418   a cautionary approach to managing this species, triaging water delivery as though all wetland

419   populations exist in isolation.

420

421   *Environmental water provision*

422   In highly regulated catchments, restoring large-scale historic inundation patterns is neither

423   possible nor desirable. However, providing specific reaches and wetlands with environmental

424   water can recreate critical components of historic flow regimes. The assumption is that

425   reconstructing specific components of 'natural' flow, can maintain key ecosystem processes

426   through the timely, sequential ecological cues inherent in 'natural' flow (Poff *et al.* 1997). In

427   highly modified and non-stationary conditions, a more mechanistic understanding of

428   environmental water requirements is valuable (Poff 2018). An alternative approach uses

429   thresholds of inundation frequency, and in turn extinction probability to prioritise the delivery

430   of 'designer' flow. When well-designed, this approach generates efficiencies in the volumes

431   of water delivered while still eliciting the desired ecological response (in this case, a

432   reduction in the probability of extinction for target amphibian populations).

433   Our model shows that water deliveries maintaining no more than one sequential dry

434   year will support *L. raniformis* (**Figure 6**). For wetlands with low extinction probability, or

435   when environmental water budgets are limiting, water provision to ensure no more than two

436   succussive dry years will maintain extinction risk < 0.25 in all wetland sizes. Using this

437   approach, a rotating roster of wetlands could be watered to offset individual wetland risk,

438   noting that local extinctions will likely rely on dispersal from neighbouring wetlands to re-

439   establish. The highest priorities for intervention are wetlands that have experienced four or

440   five years without recruitment and where *L. raniformis* is still present (**Figure 6**). These

441   populations should be watered during the next breeding season to reduce the probability of

442   local extinction. These priorities are not intended to be cycled in perpetuity, especially in

443   situations where extinction risk is high. For example, a wetland with a 50% extinction

444   probability after five dry years could require several favourable years to recover before it

445   could be expected to persist through a second five-year drought.

446   Our model also makes three main assumptions regarding wet years that will influence

447   environmental water delivery: that 1. wetlands support adult frogs between breeding seasons,

448   2. breeding occurs during each wet year, and 3. wet years do not accumulate fish and

449   crustacean predators. Water delivery should be tailored to meet these assumptions, including

450   maintaining small summer pools to support adult frogs during dry years, watering to support

451   components of the vegetation community that are important for breeding, and periodic drying

452   to reduce predator densities.

453   Legality and morality of prioritisation notwithstanding, our approach informs

454   thresholds for environmental water provision that could be applied where demographic data

455   are available and where a clear relationship exists between intervention and recruitment —

456   for example, the delivery of water to extend hydroperiod in *Rana sevosa* (Seigel, Dinsmore &

457   Richter 2006) or *P. pengilleyi* (Scheele *et al.* 2012). This approach is not specific to

458   amphibians, nor to environmental water provision, and can also be applied where episodic

459   events are directly linked to reproductive outcomes, such as fire intermittency and

460   germination in pyrophytic plants, or supraseasonal flooding events in arid-zone seed

461   germination.

462

463   *Legislative protections*

464   The protection of threatened amphibians is mandated under Australian law (*Environment*

465   *Protection and Biodiversity Conservation Act, 1999*), but the primary legislation to manage

466   environmental water in the Murray-Darling catchment considers fish, birds, and vegetation,

467   but not amphibians (MDBA, 2012b). This is mirrored internationally where a review of 30

468   European environmental flow programmes does not mention amphibians (European

469   Commission 2016). Given the worsening state of amphibian populations globally, we

470   advocate for future legislative revisions to include provisions specifically for amphibians.

471

472   *Author contributions*

473   R.M., C.J.A.B. and M.G. designed the modelling approach. All authors contributed to the

474   manuscript.

475

476   *Acknowledgements*

477   We thank the Murraylands and Riverland Landscapes Board and the Nature Foundation SA

478   for their generous support and the Murray-Darling Basin Authority for providing time-series

479   data of natural flow. We bring together land managers, conservation organisations, and

480   scientists from the catchment and we have consulted with amphibian and environmental

481   water specialists from across Australia.

482

483   *Data Availability Statement*

484   Data and code available from:
485   https://github.com/RupertLovesEcology/RiverRegulation_Frog_PopModel

486

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Supporting Information 1. To examine the effects of maximum lifespan on the predicted probability of extinction, we applied a single-parameter perturbation (sensitivity) analysis on a single modelled scenario (a large wetland with a sill height of 7.5 metres with respect to the Australian Height Datum (mAHD) under a river regulation flow scenario).

Figure S1. The Leslie matrix (L1) assigns fertility to age classes 1 – 5 in the top row and age-specific annual survival probability on the sub-diagonal.

Figure S2. Inhibition of egg laying at a wetland follows an exponential decay function. If the total number of eggs laid is greater than 0.8 of the wetland's carrying capacity, subsequent eggs are reduced at an increasing rate.

669

670   **Figure S3.** Compensatory density feedback on survival rate of eggs to the 1-year age class
671   and survival of the 1-year age class to the 2-year age class based on an exponential decay
672   function. Reduction of survival probability starts when the population exceeds 0.3 of carrying
673   capacity.

674

675

676