



Minerva Access is the Institutional Repository of The University of Melbourne

**Author/s:**

Heard, GW;McCarthy, MA;Scroggie, MP;Baumgartner, JB;Parris, KM

**Title:**

A Bayesian model of metapopulation viability, with application to an endangered amphibian

**Date:**

2013-06-01

**Citation:**

Heard, G. W., McCarthy, M. A., Scroggie, M. P., Baumgartner, J. B. & Parris, K. M. (2013). A Bayesian model of metapopulation viability, with application to an endangered amphibian. *Diversity and Distributions*, 19 (5-6), pp.555-566. <https://doi.org/10.1111/ddi.12052>.

**Persistent Link:**

<https://hdl.handle.net/11343/216918>

1 **A Bayesian model of metapopulation viability, with application to an**  
2 **endangered amphibian**

3  
4 *This paper is a contribution to the special issue on: ‘Perspectives and tools for conservation risk*  
5 *analysis’*

6  
7 Geoffrey W. Heard

8 School of Botany, University of Melbourne, Victoria, AUSTRALIA 3010.

9 Ph: +61 3 9035 7522

10 Email: heardg@unimelb.edu.au

11  
12 Michael A. McCarthy

13 School of Botany, University of Melbourne, Victoria, Australia 3010.

14  
15 Michael P. Scroggie

16 Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment,  
17 P.O. Box 137, Heidelberg, Victoria, AUSTRALIA 3084

18  
19 John B. Baumgartner

20 School of Botany, University of Melbourne, Victoria, Australia 3010.

21  
22 Kirsten M. Parris

23 School of Botany, University of Melbourne, Victoria, Australia 3010.

24  
25 **Running title:** A Bayesian SPOM

26 **Article type:** Biodiversity Research and Reviews

27 **Keywords:** amphibian, Bayesian, metapopulation, risk, regression, SPOM, viability.

28 **Abstract**

29 **Aim:** Population viability analysis (PVA) is used to quantify the risks faced by species under  
30 alternative management regimes. Bayesian PVAs allow uncertainty in the parameters of the  
31 underlying population model to be easily propagated through to the predictions. We developed a  
32 Bayesian stochastic patch occupancy model (SPOM), and used this model to assess the viability of a  
33 metapopulation of the growling grass frog (*Litoria raniformis*) under different urbanisation scenarios.

34 **Location:** Melbourne, Victoria, Australia.

35 **Methods:** We fitted a Bayesian model that accounted for imperfect detection to a multi-season  
36 occupancy dataset for *L. raniformis* collected across northern Melbourne. The probability of  
37 extinction was modelled as a function of effective wetland area, aquatic vegetation cover and  
38 connectivity, using logistic regression. The probability of colonisation was modelled as a function of  
39 connectivity alone. We then simulated the dynamics of a metapopulation of *L. raniformis* subject to  
40 differing levels of urbanisation and compensatory wetland creation. Uncertainty was propagated by  
41 conducting simulations for 5000 estimates of the parameters of the models for extinction and  
42 colonisation.

43 **Results:** There was considerable uncertainty in both the probability of quasi-extinction and the  
44 minimum number of occupied wetlands under most urbanisation scenarios. Uncertainty in the change  
45 of quasi-extinction risk and the minimum metapopulation size increased with increasing habitat loss.  
46 For our focal metapopulation, the analysis revealed that investment in six or more wetlands may be  
47 required to offset the impacts of urbanisation.

48 **Main conclusions:** Bayesian approaches to PVA allow parametric uncertainty to be propagated and  
49 considered in management decisions. They also provide means of identifying parameters that  
50 represent critical uncertainties, and, through the use of informative priors, can easily assimilate new  
51 data to reduce parametric uncertainty. These advantages, and the ready availability of software to run  
52 Bayesian analyses, will ensure that Bayesian approaches are used increasingly for PVAs.

## 53 **Introduction**

54 Even the simplest conservation decisions may entail considerable uncertainty. The complexity of  
55 ecological processes and their inherently stochastic nature ensures that the response of populations or  
56 communities to particular management actions cannot be assessed in a purely mechanistic  
57 framework (Williams *et al.*, 2002). Instead, conservation biologists turn to probabilistic approaches  
58 to explore the risks associated with particular management decisions. They seek to estimate the  
59 probability that an adverse event will occur in the future under a particular management scenario,  
60 given a mathematical model of the system, and known or plausible sources of stochasticity  
61 (Burgman *et al.*, 1993). In many cases, the uncertainty captured by this approach relates only to the  
62 stochasticity of the modelled dynamics, but incorporating uncertainty in the model itself is also  
63 important. Doing so allows known uncertainty around the estimated risk to be considered in  
64 management decisions, and highlights areas where better knowledge of the system is required to  
65 reduce that uncertainty (Burgman, 2005).

66

67 Population viability analysis (PVA) remains an important form of risk analysis for the management  
68 of threatened species. PVA is the quantitative evaluation of factors that influence population growth  
69 and persistence for single species (Boyce, 1992; Lindenmayer *et al.*, 1995; McCarthy & Possingham,  
70 in press). Early incarnations were focussed on single populations, and sought to estimate the  
71 probability of extinction for small populations subject to environmental, demographic and genetic  
72 stochasticity (Soulé, 1987; Beissinger, 2002). Contemporary PVAs are designed for more  
73 complicated problems, and incorporate more complicated dynamics. Because many threatened  
74 species display some population sub-division, and because habitat fragmentation is near ubiquitous  
75 as a threatening process, PVAs that incorporate multiple interacting populations (metapopulations)  
76 have now largely replaced PVAs focussed on a single population (Morris & Doak, 2002). These  
77 models allow migration between the component populations, and may also incorporate such things as

78 spatially-variable demographic parameters, habitat dynamics, and spatially-correlated disturbance  
79 regimes (McCarthy, 2009). The application of these models is now less concerned with the outright  
80 risk of extinction, and instead focuses on comparative risks. Given a set of options for future  
81 management, analysts seek to quantify and compare the relative risk of extinction under each (e.g.,  
82 Lindenmayer & Possingham, 1996; Akçakaya & Raphael, 1998; Drechsler *et al.*, 2003).  
83 Alternatively, they may seek to optimise viability subject to budget constraints. In these situations,  
84 the candidate set of management options is not predefined; rather the analyst is charged with  
85 identifying the combination of management actions that minimizes the probability of extinction for a  
86 set budget (e.g., Moilanen & Cabeza, 2002).

87

88 While the use of PVA to predict the relative risk of extinction should be more robust to uncertainty  
89 than predictions of outright extinction risk (McCarthy *et al.*, 2003), propagating uncertainty through  
90 to the model predictions remains desirable for such analyses (Morris & Doak, 2002). Numerous  
91 uncertainties may influence a given PVA, but parametric uncertainty is ubiquitous. Parametric  
92 uncertainty arises from sampling variation, observer bias, and sampling error in empirically derived  
93 population models, and through differences of opinion for models parameterised using expert  
94 knowledge (McGowan *et al.*, 2011). Despite its ubiquity, accounting for parametric uncertainty in  
95 PVAs has proven technically challenging, and somewhat contentious (Wade, 2002). Bayesian  
96 approaches are becoming an increasingly popular means of performing PVAs as a result, because  
97 they allow straightforward propagation of parametric uncertainty through to model predictions  
98 (Ludwig, 1996; Wade, 2002; McCarthy, 2007). Bayesian statistical methods represent uncertainty in  
99 model parameters by using probability distributions, with the width of a parameter's distribution  
100 representing the imprecision of the associated estimate (McCarthy, 2007). Importantly, Bayesian  
101 methods recognise that information about a parameter accumulates over time. The prior distribution  
102 represents what is known about a parameter before considering the latest set of data. The information

103 in the data about the parameters is combined with the prior using Bayes' rule, generating the  
104 posterior distribution (McCarthy, 2007). Propagating parametric uncertainty in Bayesian PVA is  
105 simply a matter of simulating the dynamics of the focal population/s for combinations of parameter  
106 values drawn from their joint posterior distributions, thereby providing a distribution for the chosen  
107 viability metric that represents uncertainty due to imprecision in the parameters, as well as that due  
108 to stochasticity of the modelled dynamics.

109

110 In the metapopulation literature, Bayesian approaches to PVA have primarily been pursued in the  
111 context of stochastic patch occupancy models, or SPOMs. These models are designed for the  
112 situation in which population extinction is commonplace, and persistence of the metapopulation  
113 relies upon a balance between the rate of population extinction and the rate of colonisation of vacant  
114 habitat patches (Sjögren-Gulve & Hanski, 2000; Hanski, 2002). Rather than attempting to model the  
115 internal demographic processes of the constituent populations, SPOMs describe the stochastic  
116 changes in population occurrence arising from population extinction and colonisation (Sjögren-  
117 Gulve & Hanski, 2000; Hanski, 2002). The most well known and widely applied SPOM is the  
118 incidence function model (IFM) pioneered by Hanski (1994). Hanski's model incorporates the key  
119 effects of patch area and isolation on the probabilities of extinction and colonisation (see Hanski,  
120 1999), and was the first to allow simulation of the dynamics of real metapopulations subject to  
121 habitat loss, degradation and fragmentation. Bayesian formulations of the IFM have been offered by  
122 O'Hara *et al.* (2002), ter Braak & Etienne (2003), Harrison *et al.* (2011) and Risk *et al.* (2011).

123

124 Nevertheless, the application of the IFM to conservation planning has been criticized. The reasons  
125 are various, ranging from arguments against the generality of the patch area and isolation paradigm  
126 (Pellet *et al.*, 2007), to technical concerns such as the need to assume stationarity of extinction and  
127 colonisation rates when estimating the parameters of the model using occupancy data (Thomas,

128 1994). While these concerns are by no means fatal to the IFM, they do point to a need for alternative  
129 approaches when the shortcomings of the IFM are not trivial. One option is to model the  
130 probabilities of population extinction and colonisation directly (Sjögren-Gulve & Ray, 1996;  
131 Sjögren-Gulve & Hanski, 2000; Morris & Doak, 2002). The idea is simple – given an adequate  
132 sample of extinction and colonisation events, one may build regression models of relationships  
133 between the probabilities of extinction and colonisation and particular patch- and landscape-level  
134 variables thought to influence these processes. Arbitrarily complex linear and non-linear  
135 relationships can be incorporated, providing considerable flexibility for model development. As  
136 demonstrated by Sjögren-Gulve & Ray (1996), the resulting regression models for the probabilities  
137 of population extinction and colonisation can be used to simulate the dynamics of real  
138 metapopulations in the same way as the IFM, and therefore offer the same opportunities to predict  
139 the viability of real metapopulations subject to habitat change (see also Sjögren-Gulve & Hanski,  
140 2000; Morris & Doak, 2002).

141

142 Here we present a Bayesian version of the regression approach introduced by Sjögren-Gulve & Ray  
143 (1996), and use it to assess the viability of a metapopulation of an endangered frog from southern  
144 Australia. This is, to our knowledge, the first time a Bayesian formulation of Sjögren-Gulve & Ray's  
145 approach to metapopulation viability analysis has been presented. We demonstrate how the Bayesian  
146 formulation allows parametric uncertainty to be easily propagated through to predictions of  
147 metapopulation viability under differing scenarios of habitat loss and creation.

148

## 149 **Methods**

### 150 *The approach*

151 Before proceeding to the technical aspects of our approach, we first briefly expand on the theoretical  
152 basis of SPOMs. Classical metapopulation theory assumes networks of spatially discrete populations  
153 connected by infrequent dispersal. Within these networks, populations are prone to extinction given  
154 sensitivity to demographic, genetic and environmental stochasticity, but these extinctions may be  
155 offset by colonisation of vacant habitat patches. Population extinction and colonisation are thus  
156 random events, but the probabilities of extinction and colonisation vary among patches and over  
157 time. The probability of extinction is modeled as a function of population size and, in some cases,  
158 immigration rate (the ‘rescue effect’ *sensu* Brown & Kodric-Brown, 1977). The probability of  
159 colonisation is modeled as a function of the number of immigrants. Spatially-realistic SPOMs are  
160 based on the premise that particular patch- and landscape-scale variables may be used as surrogates  
161 for population size and immigration rate (Hanski, 1994; Sjögren-Gulve & Ray, 1996). The most  
162 basic of these relationships are encapsulated by the IFM: population size scales with patch area, and  
163 immigration rate depends on the number, proximity and size of neighboring populations (‘isolation’,  
164 or, conversely, ‘connectivity’). However, additional variables are likely to be important determinants  
165 of population size and immigration rate in some circumstances. When patch quality is highly  
166 variable, even small patches may have high carrying capacities (Fleishman *et al.*, 2002). Similarly,  
167 the surrounding landscape could be more or less permeable to migrants, in which case the number of  
168 immigrants arriving at a patch will only partly reflect its proximity to neighbouring populations  
169 (Wiens, 1997).

170

171 As above, the approach of Sjögren-Gulve & Ray (1996) is predicated on the use of regression  
172 models to describe relationships between the probabilities of extinction and colonisation and patch-  
173 and landscape-scale variables thought to influence population size and immigration rate. Applying  
174 the logit link, the probability of extinction ( $\varepsilon$ ) for population  $i$  at time  $t$  is modelled as:

175 
$$\text{logit}(\varepsilon_{i,t}) = \alpha_{\varepsilon} + \beta_{\varepsilon 1}(X_{1,i,t-1}) + \beta_{\varepsilon 2}(X_{2,i,t-1}) + \dots + \beta_{\varepsilon N}(X_{N,i,t-1}), \quad (\text{Eq. 1})$$

176 where  $\alpha_\varepsilon$  is the intercept term,  $X_{1,i,t-1}$ ,  $X_{2,i,t-1}$ , and  $X_{N,i,t-1}$  are values for the relevant patch- and  
177 landscape-scale variables at the preceding time-step, and  $\beta_{\varepsilon 1}$ ,  $\beta_{\varepsilon 2}$ , and  $\beta_{\varepsilon N}$  are regression coefficients.  
178 Likewise, the probability of colonisation ( $\gamma$ ) for patch  $i$  at time  $t$  is modelled as:

$$\text{logit}(\gamma_{i,t}) = \alpha_\gamma + \beta_{\gamma 1}(Z_{1,i,t-1}) + \beta_{\gamma 2}(Z_{2,i,t-1}) + \dots + \beta_{\gamma N}(Z_{N,i,t-1}). \quad (\text{Eq. 2})$$

181 Sjögren-Gulve & Ray (1996) describe how the parameters of Eq. 1 and Eq. 2 may be estimated using  
182 maximum likelihood when data on occupancy turnover between two time-steps are available.

183 However, as Sjögren-Gulve & Ray acknowledge, their approach assumes that the focal species is  
184 detected without error; an assumption that may be problematic for many species (Tyre *et al.*, 2003;  
185 MacKenzie *et al.*, 2006). Recent advances in occupancy modelling circumvent this problem.

186 Mackenzie *et al.* (2003) provided an approach in which maximum likelihood estimates of the  
187 probabilities of extinction and colonisation may be derived from multi-year occupancy datasets,  
188 whilst accounting for imperfect detection. Although the data requirements are slightly different  
189 (repeat survey data within years being required to jointly estimate the probability of detection), the  
190 approach of Mackenzie *et al.* (2003) is similar to that of Sjögren-Gulve & Ray (1996), because the  
191 probabilities of extinction and colonisation may be modelled as functions of covariates using the  
192 logit link function.

194 Royle & Kéry (2007) provided a Bayesian state-space formulation of the dynamic occupancy model  
195 of Mackenzie *et al.* (2003) which allows the posterior distribution of the parameters of equations 1  
196 and 2 to be derived using Markov chain Monte Carlo (MCMC) sampling. Royle & Kéry (2007)  
197 implemented their method using *WinBUGS* (Lunn *et al.*, 2000), but it is also directly transferable to  
198 *OpenBUGS* (the open-source version of *WinBUGS*; Thomas *et al.*, 2006) and may also be  
199 implemented in *JAGS* (an alternative program for fitting Bayesian models using MCMC sampling;  
200 Plummer, 2003) with only minor alteration.

201

202 Once estimates of the parameters of equations 1 and 2 have been derived using MCMC sampling,  
203 they can be inserted into the standard equation for changes in patch occupancy to define a SPOM.

204 The standard equation is (MacKenzie *et al.*, 2003):

$$205 \quad O_{i,t+1} = o_{i,t} (1 - \varepsilon_{i,t}) + (1 - o_{i,t})\gamma_{i,t}, \quad (\text{Eq. 3})$$

206 where  $O_{i,t+1}$  is the probability of occupancy of patch  $i$  at time  $t+1$ ,  $o_{i,t}$  is the occupancy status of patch  
207  $i$  at time  $t$  (1 if occupied, 0 otherwise), and  $\varepsilon_{i,t}$  and  $\gamma_{i,t}$  are the probabilities of extinction and  
208 colonisation for patch  $i$  at time  $t$ , as defined by equations 1 and 2. Thus, the probability of occupancy  
209 at time  $t+1$  is equal to the probability of colonisation ( $\gamma_{i,t}$ ) if the patch was unoccupied at the previous  
210 time step, and is equal to the probability of persistence ( $1 - \varepsilon_{i,t}$ ) if the patch was occupied. Using the  
211 resulting model to simulate the dynamics of the metapopulation over a chosen time period is  
212 straightforward. For one time step to the next, the process is as follows: (i) estimate the probability of  
213 occupancy for each patch at the second time-step ( $O_{i,t+1}$ ), according to the occupancy status in the  
214 first time step ( $o_{i,t}$ ) and the probabilities of population extinction ( $\varepsilon_{i,t}$ ) and colonisation ( $\gamma_{i,t}$ ); (ii) set  
215 occupancy of each patch at the second time-step as the outcome of a Bernoulli trial with probability  
216  $O_{i,t+1}$ , and; (iii) record the occupancy status of each patch at the second time-step. In order to  
217 incorporate parametric uncertainty, these simulations are simply repeated for each of the sample of  
218 parameter values derived from the MCMC algorithm.

219

220 By running many simulations for each parameter combination and recording the number of occupied  
221 patches through time for each simulation, one can estimate of the probability of extinction or quasi-  
222 extinction for the metapopulation through time (Hanski, 2002). For each parameter combination, the  
223 probability of extinction is simply the proportion of simulations in which the metapopulation reached  
224 zero occupied patches. Similarly, the probability of quasi-extinction is estimated as the proportion of  
225 simulations in which the metapopulation declined below some threshold patch occupancy (e.g.,  $< 5$

226 occupied patches). Of course, alternate measures of metapopulation viability could also be derived  
227 from the simulations, such as the expected minimum number of occupied patches. This measure is  
228 equivalent to the expected minimum population size in demographic PVAs, and gives a better  
229 indication of the propensity for decline when the risk of extinction is small (McCarthy & Thompson,  
230 2001). Regardless of the metric used, uncertainty may be presented as the full distribution of  
231 estimates across the parameter combinations, or through a summary of this distribution, such as the  
232 mean and 95% credible interval.

233

#### 234 *Case study*

235 The growling grass frog (*Litoria raniformis*) is an endangered frog that occurs throughout south-  
236 eastern Australia (Pyke, 2002). In the vicinity of Melbourne, the capital city of Victoria, urban  
237 expansion is a key threat to this species. Numerous remnant populations occur in areas slated for  
238 urban growth, and associated wetland loss, degradation and fragmentation may place  
239 metapopulations of *L. raniformis* at considerable risk of extinction (Heard *et al.*, 2012a, b).

240 Developing a model of the extinction and colonisation dynamics of *L. raniformis* has subsequently  
241 been identified as a priority for understanding the species' conservation requirements (Heard *et al.*,  
242 2012b).

243

244 We built a Bayesian regression-based SPOM for *L. raniformis* using occupancy data from 167  
245 wetlands monitored across northern Melbourne between the 2001/2002 and 2006/2007 breeding  
246 seasons (Heard *et al.*, 2012b). Wetlands included slow-flowing pools along streams, swamps, ponds,  
247 farm dams and quarry pits. All wetlands were surveyed on between one and four occasions in the  
248 first and last years of the study (with the exception of four wetlands that were destroyed before the  
249 final year), and a subset surveyed on up to 10 occasions in the intervening years. A total of 1380  
250 surveys were completed.

251

252 We began by identifying patch- and landscape-scale variables that influence the extinction and  
253 colonisation dynamics of *L. raniformis*. For the purposes of this paper, we focussed on a model in  
254 which the probability of extinction was a function of effective wetland area, aquatic vegetation cover  
255 and connectivity, and the probability of colonisation was a function of connectivity alone. Effective  
256 area ( $A_{eff}$ ) was defined as:

$$257 \quad A_{eff_i} = \frac{\log(A_i) \times H_i}{H_{max}}, \quad \text{Eq. 4}$$

258 where  $A_i$  is the surface area of wetland  $i$ ,  $H_i$  is the hydroperiod of wetland  $i$  measured on an ordinal  
259 scale between 1 (temporarily fills only during high rainfall periods) and 4 (permanently inundated,  
260 regardless of rainfall variability), and  $H_{max}$  is the maximum hydroperiod score (4). Adjusting wetland  
261 area for hydroperiod accounted for the fact that wetland carrying capacity should be closely tied to  
262 fluctuations in water-level for *L. raniformis*, due to its highly aquatic nature (Heard *et al.*, 2008;  
263 Heard *et al.*, 2012b). Aquatic vegetation cover is considered a key microhabitat for both larval and  
264 adult *L. raniformis*, and therefore represents a key patch quality variable for the species (Hamer &  
265 Organ, 2008; Heard *et al.*, 2008; Wassens *et al.*, 2010). Aquatic vegetation cover for each wetland  
266 ( $V_i$ ) was defined as the mean cover of emergent, submergent and floating aquatic vegetation. After  
267 Heard *et al.* (2012b), connectivity of each wetland in each year ( $S_{i,t}$ ) was defined as:

$$268 \quad S_{i,t} = \sum w_{i,j} \times o_{j,t}, \quad \text{Eq. 5}$$

269 where  $w_{i,j}$  is a weighting function, and  $o_{j,t}$  is the occupancy status of each neighbour  $j$  in year  $t$  (one if  
270 the wetland is occupied, zero if not). For years 2–6, calculation of connectivity was complicated by  
271 the fact that some wetlands were not surveyed in those years, whilst others had been destroyed.  
272 When occupancy data were not available for a wetland in a given year, the outcome of the nearest  
273 preceding survey for that wetland was used instead. Wetlands that had been destroyed were simply  
274 removed from connectivity calculations for the years following their destruction. The weighting

275 function,  $w_{i,j}$ , defines a negative power relationship between the probability of dispersal from  
276 wetland  $i$  to  $j$  and the Euclidean distance between their centres ( $d_{i,j}$ , at 10 m increments). This  
277 function, derived by Heard *et al.* (2012b) using mark-recapture data, was:

$$278 \quad w_{i,j} = 0.10026 d_{i,j}^{-0.719877} . \quad (\text{Eq. 6}).$$

279 Connectivity ( $S_{i,t}$ ) was log-transformed for further analyses.

280

281 Using the approach of Royle & Kéry (2007), we fitted a dynamic occupancy model to these data in  
282 which the logits of the probabilities of extinction and colonisation were modelled as additive, linear  
283 functions of the above variables. The logit of the probability of detection was set as an additive,  
284 linear function of survey effort (person minutes), date (days since October 1) and time of day (day or  
285 night) following Heard *et al.* (2012b). Vague, normally-distributed priors (N[0, 0.001]) were used for  
286 all model parameters. Convergence was assessed by visually inspecting the histories of two Markov  
287 chains with over-dispersed initial values. Convergence was achieved within 25,000 MCMC samples.  
288 We extracted the subsequent 5000 estimates of the parameters of the model. Model fitting was  
289 completed with *OpenBUGS* v. 3.0.3, called from *R* v. 2.12.0 (R Development Core Team, 2012)  
290 using the add-in package *BRugs* v. 0.5-3 (Ligges, 2008). Code for running the analysis is provided in  
291 Appendix S1 of the Supporting Information. Table S1 gives summary statistics for the posterior  
292 distributions of the model parameters, and Fig. S1 shows the fitted relationships.

293

294 The parameter estimates were used to assess the viability of a metapopulation of *L. raniformis*  
295 located in Donnybrook, on Melbourne's northern fringe. This metapopulation occupies a reasonably  
296 discrete cluster of 30 wetlands, including pools along the Merri and Kalkallo Creeks, and farm dams  
297 within 500 m of these creeks (Fig. 1). Many of these wetlands were included in the broader study of  
298 Heard *et al.* (2012b), meaning that estimates of  $A_{eff}$  and  $V$  were already available. Estimates of  $A_{eff}$

299 and  $V$  for wetlands that were not surveyed by Heard *et al.* (2012b) were acquired in a subsequent  
300 study (Heard & McCarthy, 2012). The only other information required to simulate the dynamics of  
301 the metapopulation were the coordinates of wetland centres and the initial occupancy status of each  
302 wetland. For simplicity, we assumed all wetlands were occupied at the initial time-step.  
303  
304 The dynamics of the Donnybrook metapopulation were simulated for a period of 30 years under  
305 three broad scenarios. The first (referred to hereafter as ‘current conditions’) entailed no change in  
306 wetland number or condition over this period (Fig. 1). In the second scenario, we deleted dams in  
307 accordance with urban growth plans for Donnybrook (DPCD, 2009). These plans involve the  
308 maintenance of riparian reserves for conservation purposes and for public parkland, although the size  
309 of these reserves is yet to be finalised. We trialled riparian reserves ranging from 500 m either side of  
310 both creeks, to 100 m either side, at 100 m increments (Fig. 1). In the final scenario, we assessed the  
311 ability of replacement wetlands to offset the losses expected under a 200 m riparian reserve scenario.  
312 One to four pairs of wetlands were placed in the riparian reserve, next to central, high-quality patches  
313 (Fig. 1). Each new wetland was set to have the same features:  $A = 1250$  sq. m,  $H = 3$ ,  $V = 60\%$ .  
314 These schemes sought to create clusters of populations which would display high probabilities of  
315 occupancy through time. We assumed that the dynamics of *L. raniformis* within created wetlands  
316 could be adequately described by our model, as the majority of lentic wetlands monitored in the  
317 previous occupancy study were artificial (farm dams, ponds and quarries).  
318  
319 For each of these scenarios, we ran 500 simulations for each of the 5000 combinations of the model  
320 parameter estimates. For each simulation run for each combination of parameter estimates, we  
321 recorded the minimum number of occupied wetlands across the 30 year time period. The mean  
322 minimum number of occupied wetlands (*minocc*) was calculated by averaging over the 500  
323 simulations for each scenario and parameter estimate combination. We defined the metapopulation

324 as having gone quasi-extinct during a simulation run if fewer than three wetlands were occupied at  
325 any time-step. The probability of quasi-extinction ( $qe$ ) for each scenario and parameter estimate  
326 combination was then simply the proportion of the 500 simulations in which quasi-extinction  
327 occurred. Change in the probability of quasi-extinction ( $\Delta qe$ ) and mean minimum number of  
328 occupied wetlands ( $\Delta minocc$ ) was calculated for each scenario and parameter estimate as:

$$329 \quad \Delta qe_i = qe_i - qe_c, \quad (\text{Eq. 7})$$

330 and

$$331 \quad \Delta minocc_i = minocc_i - minocc_c, \quad (\text{Eq. 8})$$

332 where  $qe_i$  is the probability of quasi-extinction for scenario  $i$ ,  $qe_c$  is the probability of quasi-  
333 extinction assuming no change from current conditions,  $minocc_i$  is the mean minimum number of  
334 occupied wetlands for scenario  $i$ , and  $minocc_c$  is the mean minimum number of occupied wetlands  
335 assuming no change from current conditions. Simulations were run in  $R$ , using code provided in  
336 Appendix S2.

337

## 338 **Results**

339 There was considerable uncertainty in the estimates of the minimum number of occupied wetlands  
340 ( $minocc$ ) for the Donnybrook metapopulation of *L. raniformis* given either the maintenance of  
341 current conditions or the maintenance of a 500 m riparian reserve (Fig. 2). The 95% CI for  $minocc$   
342 was ~3–18 for both scenarios. Uncertainty in this metric declined with increasing levels of  
343 urbanisation due to the reduced size of the metapopulation. Importantly, both the mean estimate and  
344 upper 95% CI of  $minocc$  fell substantially between the 500 m to 400 m reserve scenarios (Fig. 2); a  
345 result of the fact that the 400 m reserve entails the loss of three large farm dams (see Fig. 1). There  
346 was also little difference between the 300 m to 100 m reserve scenarios for  $minocc$  (Fig. 2), as most  
347 dams lost across these scenarios were small, shallow and lacked aquatic vegetation. Mean estimates

348 suggest that the probability of quasi-extinction ( $qe$ , defined as less than three occupied wetlands)  
349 would be  $< 0.2$  for this metapopulation over 30 years under all scenarios (Fig. 2). However, the  
350 uncertainty in these estimates was very large for the 400 m to 100 m reserve scenarios; the 95% CI  
351 being at least 0–0.7 in each case. As with  $minocc$ ,  $qe$  increased between the 500 m and 400 m  
352 reserves, and stabilised thereafter.

353

354 Change in both the minimum number of occupied wetlands ( $\Delta minocc$ ) and the probability of quasi-  
355 extinction ( $\Delta qe$ ) was negligible for the 500 m riparian reserve scenario (mean estimates = -0.674 and  
356 0.003 respectively; Fig. 3). The rate of change in  $\Delta minocc$  was greatest between the 500 m to 400 m  
357 reserve scenarios, reflecting the stabilisation of  $minocc$  for the narrower reserves (Fig. 3). However,  
358 uncertainty in  $\Delta minocc$  displayed the opposite trend to  $minocc$ , with wider 95% CIs for the narrower  
359 reserves. While estimates of  $\Delta minocc$  show that the metapopulation will decline with increasing  
360 habitat loss, the 95% CI for  $\Delta qe$  overlapped zero for all reserve scenarios (Fig. 3). Hence, in each  
361 case, there was a small chance that the probability of quasi-extinction would not change from current  
362 conditions. Uncertainty in  $\Delta qe$  increased with decreasing reserve sizes, in accord with  $\Delta minocc$  (Fig.  
363 3).

364

365 Estimates of  $\Delta minocc$  and  $\Delta qe$  for the Donnybrook metapopulation given the creation of new  
366 wetlands are depicted in Fig. 4. Recall that a 200 m riparian reserve is assumed in each case. Mean  
367 estimates of  $\Delta minocc$  suggest that the creation of six to eight new wetlands is required to offset the  
368 loss of wetlands outside of the 200 m reserve. However, the lower bound of the 95% CI for  $\Delta minocc$   
369 was -1.9 with the creation of six new wetlands, suggesting that the metapopulation could still decline  
370 under this scenario. Only with the creation of eight wetlands was the lower bound of the 95% CI for  
371  $\Delta minocc$  above zero (0.36). Estimates of  $\Delta qe$  present a slightly different picture of the response of  
372 this metapopulation to wetland creation (Fig. 4). In all cases, the mean estimates of  $\Delta qe$  were close to

373 zero (-0.018–0.024), suggesting little change in metapopulation viability from current conditions.  
374 However, there was a rapid transition in the distribution of estimates of  $\Delta qe$  from the first scenario  
375 (two new wetlands) to the third (six new wetlands). Under the first scenario, an increase in the  
376 probability of quasi-extinction was predicted for almost all parameter combinations (95% CI of  $\Delta qe$   
377 = -0.002–0.264). The reverse was true when six new wetlands were added (95% CI of  $\Delta qe$  = -0.230–  
378 0). This rapid transition in  $\Delta qe$  stemmed from the strategic placement of the new wetlands, and the  
379 low threshold for quasi-extinction. By locating the new wetlands in pairs close to high-quality  
380 patches, clusters of persistent populations were created. With three such clusters (six new wetlands),  
381 there was a sharp drop in the chance of falling below the quasi-extinction threshold of three extant  
382 populations.

383

## 384 **Discussion**

385 Bayesian models allow straightforward propagation of parametric uncertainty through to predictions  
386 derived from these models. Previous studies have shown how Bayesian PVA models may be used to  
387 derive probability distributions for the chance of extinction or the expected minimum  
388 (meta)population size (Ludwig, 1996; Wade, 2002; ter Braak & Etienne, 2003; McCarthy, 2007).  
389 Here we have shown that uncertainty in the relative increase or decrease in these measures under  
390 alternate management scenarios is also easily calculated using Bayesian models. This is important  
391 for decision-making because the magnitude of uncertainty can influence the perceived impacts of  
392 management, and the relative performance of different options. For example, in our case study, the  
393 mean estimates of the minimum number of wetlands occupied by *L. raniformis* ( $\Delta_{minocc}$ ) and the  
394 probability of quasi-extinction ( $\Delta qe$ ) did not change markedly between the 300 m, 200 m and 100 m  
395 riparian reserve scenarios (because the wetlands lost under these scenarios were small and of  
396 relatively poor quality). As these scenarios would differ markedly in their cost to implement, it may

397 be concluded that benefits conferred by the larger reserves are not economically justified. However,  
398 our analysis also demonstrates that there is considerable and increasing uncertainty about the change  
399 in both  $\Delta minocc$  and  $\Delta qe$  as the reserve size narrows, with large decreases in metapopulation  
400 viability being plausible (Fig. 3). Documenting this uncertainty allows managers to account for it in  
401 their decisions. A risk-tolerant manager might be prepared to choose narrower reserves based on the  
402 central tendency, whereas a risk-averse manager striving for negligible impacts might impose a large  
403 riparian reserve (e.g., 500 m; Fig. 3) or demand considerable offsetting works (e.g., six to eight new  
404 wetlands; Fig. 4).

405

406 Of course, it is preferable to subject these sorts of decision-making processes to analyses in which  
407 the objectives are explicit, and uncertainty is directly integrated. Although we have not illustrated it  
408 here, Bayesian PVA models may be coupled with formal decision analyses (Possingham *et al.*, 2002;  
409 Wade, 2002; Drechsler & Burgman, 2004). For example, Drechsler *et al.* (2003) coupled a Bayesian  
410 incidence function model with a multi-criteria decision analysis to rank a set of patch retention  
411 scenarios for a metapopulation of the Glanville Fritillary Butterfly (*Melitaea cinxia*). The optimal  
412 strategy in their analysis was simply the one that showed the lowest probability of metapopulation  
413 extinction across the greatest number of parameter combinations. Alternatively, managers might seek  
414 to identify the strategy that minimizes the chance of breaching a particular threshold for the  
415 probability of quasi-extinction (e.g., > 10%), or for the number of occupied patches (e.g., < 5). In this  
416 case, the objective is not simply to identify the strategy that minimizes the risk of decline, but rather  
417 to set some standard for the trajectory of the metapopulation, and identify the strategy that minimizes  
418 the chance of breaching that standard (a form of satisficing; Simon, 1982; Burgman, 2005; McCarthy  
419 *et al.*, 2010). The task for the analyst is then to calculate the chance of breaching the threshold for the  
420 probability of quasi-extinction or number of occupied patches under each possible management

421 option. In a Bayesian analysis, these probabilities may be calculated as the proportion of the  
422 posterior distribution of the viability metric that breaches the chosen threshold.

423

424 While the above analyses are useful for identifying the best strategy when there is a single decision  
425 to be made, management of metapopulations can involve recurrent decisions about how to manage  
426 the constituent populations. Stochastic dynamic programming (SDP) is ideally suited for these  
427 situations (Possingham, 1996; Westphal *et al.*, 2003). Nevertheless, current examples of SDP do not  
428 include uncertainty in the parameters of the underlying metapopulation model. Including parametric  
429 uncertainty produces an optimization problem in which the parameter estimates, the management  
430 actions and the response of the metapopulation to those actions are all variable. While including each  
431 of these sources of uncertainty in SDP would be a valuable advance, it may prove technically  
432 challenging, or even impossible, due to the size and complexity of the optimization problem.

433

434 As well as propagating parametric uncertainty through to predictions and the resulting decision-  
435 making process, Bayesian approaches to PVA are also useful for identifying parameters that  
436 represent critical uncertainties of the underlying model. Critical uncertainties are not just highly  
437 uncertain components of the system being modelled. They are uncertainties which, if resolved, can  
438 change management decisions (Rumpff *et al.*, 2011; Runge, 2011). One option for identifying  
439 parameters that represent critical uncertainties in a Bayesian PVA is to perform analyses akin to  
440 traditional sensitivity analyses. Simulations could be run for multiple combinations of parameters  
441 drawn from their joint posterior distributions, and the management scenario which is optimal for  
442 each draw identified from the simulations. The change in the optimal scenario across the posterior  
443 distribution of each parameter could then be quantified, and used as measure of the influence of  
444 uncertainty in each parameter on management decisions. When only two management scenarios are  
445 considered, the influence of parameter uncertainty on the optimal scenario could assessed using

446 logistic regression, with the response variable being which management strategy is optimal  
447 (McCarthy *et al.*, 1995).

448

449 Bayesian methods also provide a clear path to increasing the precision of parameters that represent  
450 critical uncertainties. Because they incorporate existing knowledge by specifying a prior distribution,  
451 Bayesian approaches explicitly recognise that information about a parameter accumulates over time  
452 (McCarthy, 2007). In the context of PVA, one can envision building an initial model using vague  
453 priors and available data (as we have done here), and then periodically updating the model as  
454 monitoring data accumulate, using the posterior from the previous model as the prior in the new one.  
455 When both management and monitoring are directed at reducing uncertainty about key parameters,  
456 this should help resolve critical uncertainties. For example, in our case study, it was apparent that the  
457 relationship between connectivity and the probability of colonisation for *L. raniformis* was highly  
458 uncertain at the upper levels of connectivity, because wetlands with high connectivity were rarely  
459 unoccupied (see Fig. S1). Should an interrogation of the model reveal that this uncertainty influences  
460 the optimal management strategy, one could ensure that at least some created wetlands are placed  
461 very close to currently occupied wetlands. Subsequent monitoring of metapopulations manipulated in  
462 this way will deliver data about the rate of colonisation of highly connected wetlands, which, when  
463 combined with existing information, will reduce uncertainty about this relationship, and reduce  
464 management indecision.

465

466 This study focused on a regression-based stochastic patch occupancy model (SPOM) following  
467 Sjögren-Gulve & Ray (1996). The regression-based approach has advantages over alternatives when  
468 data are available to model extinction and colonisation probabilities directly (Sjögren-Gulve &  
469 Hanski, 2000; Morris & Doak, 2002). Model structure is highly flexible, meaning that the inclusion  
470 of patch quality variables (in particular) is easily accomplished. There is also no need to assume

471 stationarity of extinction and colonisation rates to parameterize the model using occupancy data. As  
472 well as providing a Bayesian implementation, we have shown that the approach of Sjögren-Gulve &  
473 Ray (1996) may also be extended to account for imperfect detection, given recent advances in  
474 occupancy modeling (Mackenzie *et al.* 2003, 2006; Royle & Kéry 2007). This is important, because  
475 failing to account for false absences may bias estimates of the parameters of SPOMs, and undermine  
476 their predictive power (Moilanen, 2002). Nevertheless, we did not fully account for imperfect  
477 detection in our case study. For the purposes of calculating connectivity ( $S_{i,t}$ ), we assumed that the  
478 occupancy status of each wetland by *L. raniformis* was determined perfectly in years for which  
479 survey data were available, and that occupancy status had not changed from previous years when  
480 survey data were unavailable. These assumptions were tolerable in this study, with cumulative  
481 probabilities of detection averaging  $> 0.8$  when survey data were available, and missing data being  
482 largely restricted to sites whose occupancy status was unlikely to have changed through time.  
483 Nevertheless, allowing for imperfect detection and changes in occupancy status when calculating  $S_{i,t}$   
484 will be appealing in many situations. Both can be accommodated in Bayesian occupancy models  
485 (Royle & Dorazio, 2008; Bled *et al.*, 2011; Risk *et al.*, 2011), because the occupancy status of each  
486 patch at each time-step is simulated for each iteration of the MCMC algorithm, enabling stochastic  
487 realizations of  $S_{i,t}$  to be calculated (see Appendix S1). However, this comes at considerable  
488 computational cost when the number of patches is large. The decision to include stochastic  
489 realizations of  $S_{i,t}$  in the model therefore requires consideration of the likely scale of bias induced by  
490 its exclusion, and the computational costs of including it.

491

492 Bayesian approaches to PVA explicitly incorporate and propagate uncertainty in models of  
493 population processes, allowing informed decision-making and identification of critical uncertainties  
494 in the underlying model. For these reasons, and because of the ready availability of software to fit  
495 Bayesian models, we expect interest in Bayesian approaches to PVA to continue to rise. When

496 focused on the comparative risks associated with alternate management options, and particularly  
497 when coupled with formal decision analyses that identify the optimal approach given a particular  
498 objective, these analyses have the potential to provide valuable direction to the management of  
499 threatened species.

500

## 501 **Acknowledgements**

502 Funding for this project was provided by the Victorian Department of Sustainability and  
503 Environment (DSE), the Australian Research Council Centre of Excellence for Environmental  
504 Decisions, and an Australian Research Council Linkage Grant (LP0990161) with the Australian  
505 Research Centre for Urban Ecology, DSE, Growling Grass Frog Trust Fund, Melbourne Museum,  
506 Melbourne Water and Parks Victoria. MM was supported by an Australian Research Council Future  
507 Fellowship. We thank Adam Muir and Kim Lowe (DSE) for their support of the project. Stefano  
508 Canessa (University of Melbourne) provided coding advice and assistance. Charles Todd (DSE) and  
509 two anonymous reviewers offered useful critiques of an earlier version.

510

## 511 **References**

- 512 Akçakaya, H.R. & Raphael, M.G. (1998) Assessing human impact despite uncertainty: viability of  
513 the northern spotted owl metapopulation in the northwestern USA. *Biodiversity and*  
514 *Conservation*, **7**, 875-894.
- 515 Beissinger, S.R. (2002) Population viability analysis: past, present and future. *Population Viability*  
516 *Analysis* (ed. by S.A. Beissinger and D.R. McCullough), pp. 5-17. The University of Chicago  
517 Press, Chicago.

518 Bled, F., Royle, J.A. & Cam, E. (2011) Hierarchical modeling of an invasive spread: the Eurasian  
519 Collared-Dove *Streptopelia decaocto* in the United States. *Ecological Applications*, **21**, 290-  
520 302.

521 Boyce, M.S. (1992) Population Viability Analysis. *Annual Review of Ecology and Systematics*, **23**,  
522 481-506.

523 Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of  
524 immigration on extinction. *Ecology*, **58**, 445-449.

525 Burgman, M.A. (2005) *Risks and Decisions for Conservation and Environmental Management*.  
526 Cambridge University Press, Cambridge.

527 Burgman, M.A., Ferson, S. & Akçakaya, H.R. (1993) *Risk Assessment in Conservation Biology*.  
528 Chapman and Hall, London.

529 DPCD (2009) *Delivering Melbourne's Newest Sustainable Communities*. Victorian Department of  
530 Planning and Community Development, Melbourne.

531 Drechsler, M. & Burgman, M.A. (2004) Combining population viability analysis with decision  
532 analysis. *Biodiversity and Conservation*, **13**, 115-139.

533 Drechsler, M., Frank, K., Hanski, I., O'Hara, R.B. & Wissel, C. (2003) Ranking metapopulation  
534 extinction risk: from patterns in data to conservation management decisions. *Ecological*  
535 *Applications*, **13**, 990-998.

536 Fleishman, E., Ray, C., Sjögren-Gulve, P., Boggs, C.L. & Murphy, D.D. (2002) Assessing the roles  
537 of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation*  
538 *Biology*, **16**, 706-716.

539 Hamer, A.J. & Organ, A. (2008) Aspects of the ecology and conservation of the growling grass frog  
540 *Litoria raniformis* in an urban-fringe environment, southern Victoria. *Australian Zoologist*,  
541 **34**, 393-407.

542 Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**,  
543 151-162.

544 Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.

545 Hanski, I. (2002) Metapopulations of animals in highly fragmented landscapes and population  
546 viability analysis. *Population Viability Analysis* (ed. by S.R. Beissinger and D.R.  
547 McCullough), pp. 86-108. The University of Chicago Press, Chicago.

548 Harrison, P.J., Hanski, I. & Ovaskainen, O. (2011) Bayesian state-space modeling of metapopulation  
549 dynamics in the Glanville fritillary butterfly. *Ecological Monographs*, **81**, 581-598.

550 Heard, G.W. & McCarthy, M.A. (2012) *Metapopulation viability of the Growling Grass Frog in*  
551 *Melbourne's urban growth areas*. Report to the Victorian Department of Sustainability and  
552 Environment. University of Melbourne, Melbourne.

553 Heard, G.W., Robertson, P. & Scroggie, M.P. (2008) Microhabitat preferences of the endangered  
554 Growling Grass Frog (*Litoria raniformis*) in southern Victoria, Australia. *Australian*  
555 *Zoologist*, **34**, 414-425.

556 Heard, G.W., Scroggie, M.P. & Malone, B.S. (2012a) The life history and decline of the threatened  
557 Australian frog, *Litoria raniformis*. *Austral Ecology*, **37**, 276-284.

558 Heard, G.W., Scroggie, M.P. & Malone, B.S. (2012b) Classical metapopulation theory as a useful  
559 paradigm for the conservation of an endangered amphibian. *Biological Conservation*, **148**,  
560 156-166.

561 Ligges, U. (2008) *BRugs*. R Foundation for Statistical Computing. [http://cran.r-](http://cran.r-project.org/web/packages/BRugs/)  
562 [project.org/web/packages/BRugs/](http://cran.r-project.org/web/packages/BRugs/)

563 Lindenmayer, D.B. & Possingham, H.P. (1996) Ranking conservation and timber management  
564 options for Leadbeater's Possum in southeastern Australia using population viability analysis.  
565 *Conservation Biology*, **10**, 235-251.

566 Lindenmayer, D.B., Burgman, M.A., Akçakaya, H.R., Lacy, R.C. & Possingham, H.P. (1995) A  
567 review of the generic computer programs ALEX, RAMAS/space and VORTEX for  
568 modelling the viability of wildlife metapopulations. *Ecological Modelling*, **82**, 161-174.

569 Ludwig, D. (1996) Uncertainty and the assessment of extinction probabilities. *Ecological*  
570 *Applications*, **6**, 1067-1076.

571 Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS - a Bayesian modelling  
572 framework: concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325-337.

573 MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site  
574 occupancy, colonisation, and local extinction when a species is detected imperfectly.  
575 *Ecology*, **84**, 2200-2207.

576 MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006)  
577 *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species*  
578 *Occurrence*. Elsevier, San Diego.

579 McCarthy, M.A. (2007) *Bayesian Methods for Ecology*. Cambridge University Press, New York.

580 McCarthy, M.A. (2009) Spatial population viability analysis. *Spatial Conservation Prioritization:*  
581 *Quantitative Methods and Computational Tools* (ed. by A. Moilanen, K.A. Wilson and H.P.  
582 Possingham), pp. 122-134. Oxford University Press, New York.

583 McCarthy, M.A. & Thompson, C. (2001) Expected minimum population size as a measure of threat.  
584 *Animal Conservation*, **4**, 351-355.

585 McCarthy, M.A. & Possingham, H.P. (in press) Population viability analysis. *Encyclopedia of*  
586 *Environmetrics*, 2nd edition (ed. by A.H. El-Shaarawi and W.W. Piegorsch). Wiley-  
587 Blackwell.

588 McCarthy, M.A., Burgman, M.A. & Ferson, S. (1995) Sensitivity analysis for models of population  
589 viability. *Biological Conservation*, **73**, 93-100.

590 McCarthy, M.A., Andelman, S.J. & Possingham, H.P. (2003) Reliability of relative predictions in  
591 population viability analysis. *Conservation Biology*, **17**, 982-989.

592 McCarthy, M.A., Thompson, C.J., Hauser, C., Burgman, M.A., Possingham, H.P., Moir, M.L.,  
593 Tiensin, T. & Gilbert, M. (2010) Resource allocation for efficient environmental  
594 management. *Ecology Letters*, **13**, 1280-1289.

595 McGowan, C.P., Runge, M.C. & Larson, M.A. (2011) Incorporating parametric uncertainty into  
596 population viability analysis models. *Biological Conservation*, **144**, 1400-1408.

597 Moilanen, A. (2002) Implications of empirical data quality to metapopulation model parameter  
598 estimation and application. *Oikos*, **96**, 516-530.

599 Moilanen, A. & Cabeza, M. (2002) Single-species dynamic site selection. *Ecological Applications*,  
600 **12**, 913-926.

601 Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of*  
602 *Population Viability Analysis*. Sinauer Associates, Sunderland.

603 O'Hara, R.B., Arias, E., Toivonen, H. & Hanski, I. (2002) Bayesian analysis of metapopulation data.  
604 *Ecology*, **83**, 2408-2415.

605 Pellet, J., Fleishman, E., Dobkin, D.S., Gander, A. & Murphy, D.D. (2007) An empirical evaluation  
606 of the area and isolation paradigm of metapopulation dynamics. *Biological Conservation*,  
607 **136**, 483-465.

608 Plummer, M. (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs  
609 sampling. *3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, pp.  
610 1-10. Vienna, Austria.

611 Possingham, H.P. (1996) Decision theory and biodiversity management: how to manage a  
612 metapopulation. *Frontiers of Population Ecology* (ed. by R.B. Floyd, A.W. Sheppard and P.J.  
613 De Barro), pp. 391-398. CSIRO Publishing, Melbourne.

614 Possingham, H.P., Lindenmayer, D.B. & Tuck, G.N. (2002) Decision theory for population viability  
615 analysis. *Population Viability Analysis* (ed. by S.R. Beissinger and D.R. McCullough), pp.  
616 470-489. University of Chicago Press, Chicago.

617 Pyke, G.H. (2002) A review of the biology of the southern bell frog *Litoria raniformis* (Anura:  
618 Hylidae). *Australian Zoologist*, **32**, 32-48.

619 R Development Core Team (2012) *R: A language and environment for statistical computing*. R  
620 Foundation for Statistical Computing. <http://www.r-project.org/>

621 Risk, B.B., de Valpine, P. & Beissinger, S.R. (2011) A robust-design formulation of the incidence  
622 function model of metapopulation dynamics applied to two species of rails. *Ecology*, **92**, 462-  
623 474.

624 Royle, J.A. & Kéry, M. (2007) A Bayesian state-space formulation of dynamic occupancy models.  
625 *Ecology*, **88**, 1813-1823.

626 Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The Analysis*  
627 *of Data from Populations, Metapopulations and Communities*. Academic Press, San Diego.

628 Rumpff, L., Duncan, D.H., Vesk, P.A., Keith, D.A. & Wintle, B.A. (2011) State-and-transition  
629 modelling for adaptive management of native woodlands. *Biological Conservation*, **144**,  
630 1224-1236.

631 Runge, M.C. (2011) An introduction to adaptive management for threatened and endangered species.  
632 *Journal of Fish and Wildlife Management*, **2**, 220-233.

633 Simon, H.A. (1982) *Models of Bounded Rationality*. MIT Press, Cambridge.

634 Sjögren-Gulve, P. & Ray, C. (1996) Using logistic regression to model metapopulation dynamics:  
635 large-scale forestry extirpates the pool frog. *Metapopulations and Wildlife Conservation* (ed.  
636 by D.R. McCullough), pp. 111-137. Island Press, Washington.

637 Sjögren-Gulve, P. & Hanski, I. (2000) Metapopulation viability analysis using occupancy models.  
638 *Ecological Bulletins*, **48**, 53-71.

- 639 Soulé, M.E. (ed.) (1987) *Viable Populations for Conservation*. Cambridge University Press, New  
640 York.
- 641 ter Braak, C.J.F. & Etienne, R.S. (2003) Improved Bayesian analysis of metapopulation data with an  
642 application to a tree frog metapopulation. *Ecology*, **84**, 231-241.
- 643 Thomas, A., O'Hara, B., Ligges, U. & Sturtz, S. (2006) Making BUGS Open. *R News*, **6**, 12-17.
- 644 Thomas, C.D. (1994) Difficulties in deducing dynamics from static distributions. *Trends in Ecology  
645 and Evolution*, **9**, 300.
- 646 Tyre, A.J., Tenhumberg, B., Field, S.A., Neijalke, D., Parris, K. & Possingham, H.P. (2003)  
647 Improving precision and reducing bias in biological surveys: estimating false-negative error  
648 rates. *Ecological Applications*, **13**, 1790-1801.
- 649 Wade, P.R. (2002) Bayesian population viability analyses. *Population Viability Analysis* (ed. by S.A.  
650 Beissinger and D.R. McCullough), pp. 213-238. The University of Chicago Press, Chicago.
- 651 Wassens, S., Hall, A., Osborne, W. & Watts, R.J. (2010) Habitat characteristics predict occupancy  
652 patterns of the endangered amphibian *Litoria raniformis* in flow-regulated flood plain  
653 wetlands. *Austral Ecology*, **35**, 944-955.
- 654 Westphal, M.I., Pickett, M., Getz, W.M. & Possingham, H.P. (2003) The use of stochastic dynamic  
655 programming in the optimal landscape reconstruction for metapopulations. *Ecological  
656 Applications*, **13**, 543-555.
- 657 Wiens, J.A. (1997) Metapopulation dynamics and landscape ecology. *Metapopulation Biology:  
658 Ecology, Genetics and Evolution* (ed. by I. Hanski and M.E. Gilpin), pp. 43-62. Academic  
659 Press, San Diego.
- 660 Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *The Analysis and Management of Animal  
661 Populations*. Academic Press, San Diego.
- 662

663 **Supporting Information**

664

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

666

667 Appendix S1 {Code for fitting the occupancy turnover model and extracting parameter estimates }

668 Appendix S2 {Code for simulating the dynamics of the Donnybrook metapopulation }

669 Figure S1 {Relationships between the probability of extinction and effective wetland area, aquatic  
670 vegetation cover and connectivity, and between the probability of colonisation and connectivity }

671 Table S1 {Posteriors of the coefficients of the regression models for extinction and colonisation }

672

673 As a service to our authors and readers, this journal provides supporting information supplied by the  
674 authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not  
675 copy-edited or typeset. Technical support issues arising from supporting information (other than  
676 missing files) should be addressed to the authors.

677

678

679 **Captions to Figures**

680 **Fig. 1.** The Donnybrook metapopulation of *Litoria raniformis* under alternate management scenarios.  
681 The top panel displays the distribution of wetlands (grey circles) under current conditions, where  
682 ‘wetlands’ include pools along the Merri and Kalkallo Creeks (represented by the black trace) and  
683 adjacent farm dams. As an example of different urbanisation scenarios considered, the middle panel  
684 displays the distribution of wetlands given urbanisation (shading) of all land beyond a 400 m reserve  
685 either side of each stream. The bottom panel displays the distribution of wetlands given a 200 m  
686 riparian reserve and the construction of eight new wetlands (black circles). Numbering of the new  
687 wetlands is the modelled sequence. Co-ordinates follow the Australian Map Grid system (with WGS  
688 1994). Wetland sizes are scaled to their effective areas, but their shapes are stylised.

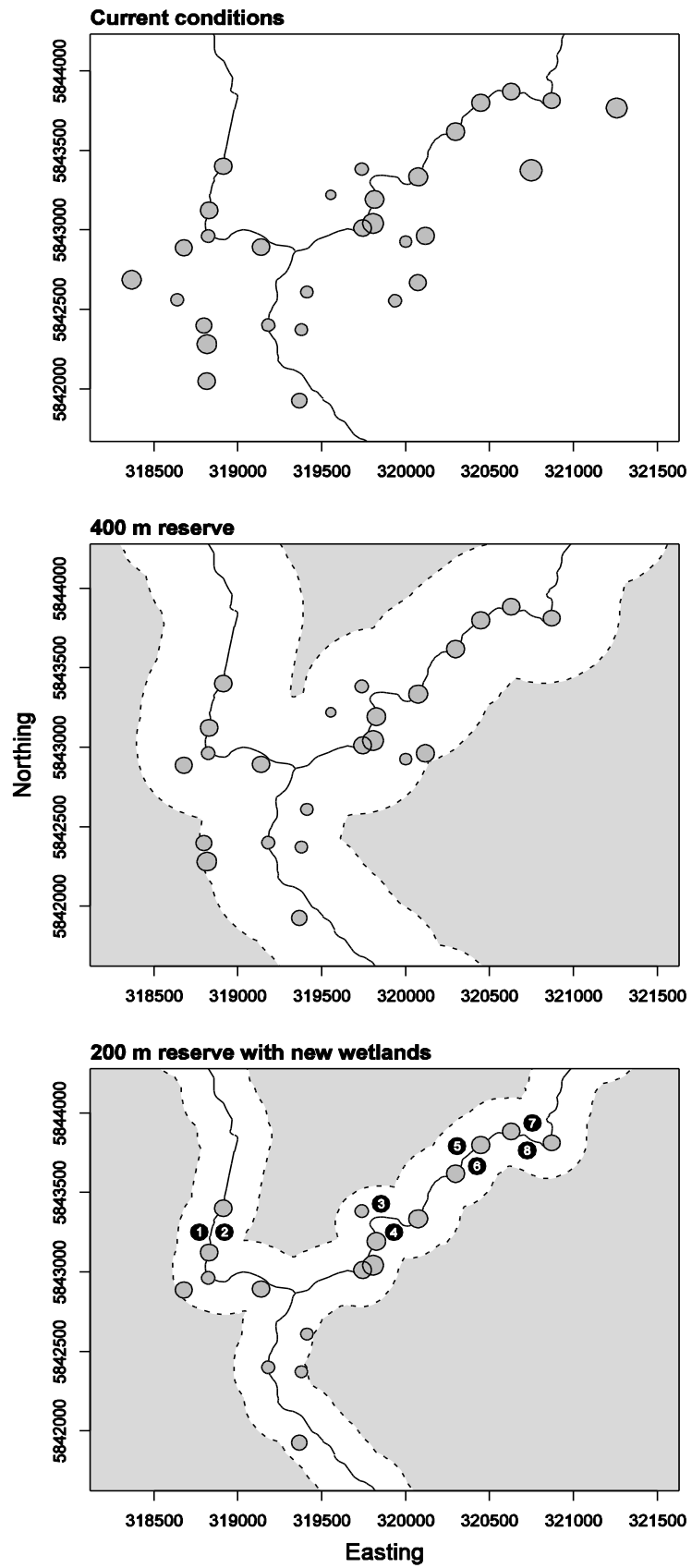
689

690 **Fig. 2.** The minimum number of occupied wetlands (*minocc*) and the probability of quasi-extinction  
691 (*qe*) for the Donnybrook metapopulation of *Litoria raniformis* over 30 years under five urbanisation  
692 scenarios. The scenarios represent maintenance of current conditions (CC) or five possible riparian  
693 reserve scenarios given urbanisation. These scenarios entail reservation of all land within 500 m of  
694 both streams in the area (‘500 m’), reservation of all land within 400 m of both streams (‘400 m’),  
695 and so on down to 100 m either side of both streams. Points represent the mean estimates, and  
696 vertical lines represent the 95% credible intervals.

697

698 **Fig. 3.** Change in both the minimum number of occupied wetlands ( $\Delta minocc$ ) and the probability of  
699 quasi-extinction ( $\Delta qe$ ) for the Donnybrook metapopulation of *Litoria raniformis* over 30 years under  
700 five urbanisation scenarios. The scenarios represent possible widths of a riparian reserve system, as  
701 in Fig. 1. A score of zero on the y-axis represents no change in *qe* or *minocc* from current conditions.  
702 Points represent the mean estimates, and vertical lines represent the 95% credible intervals.

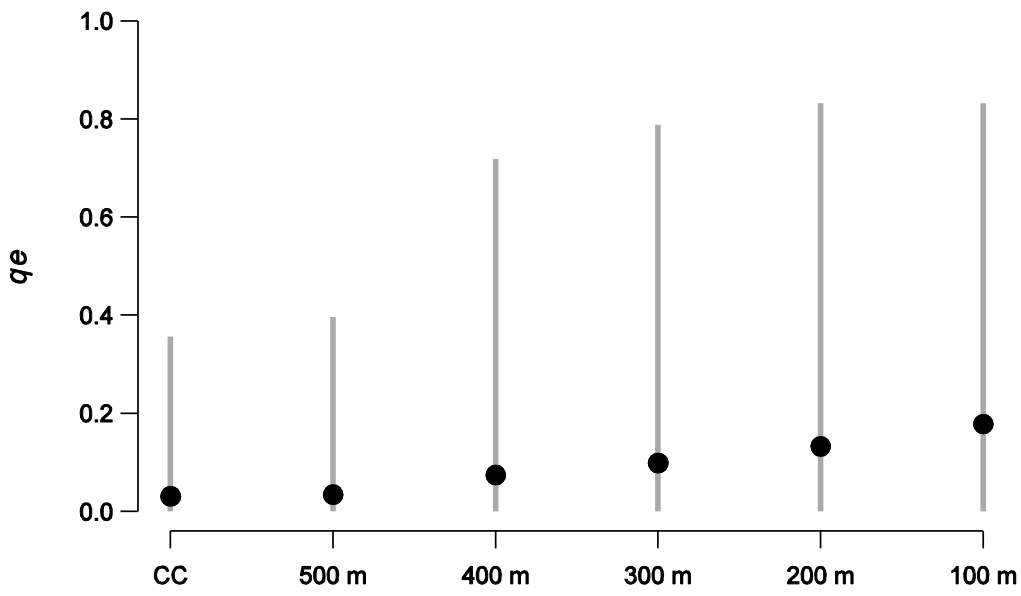
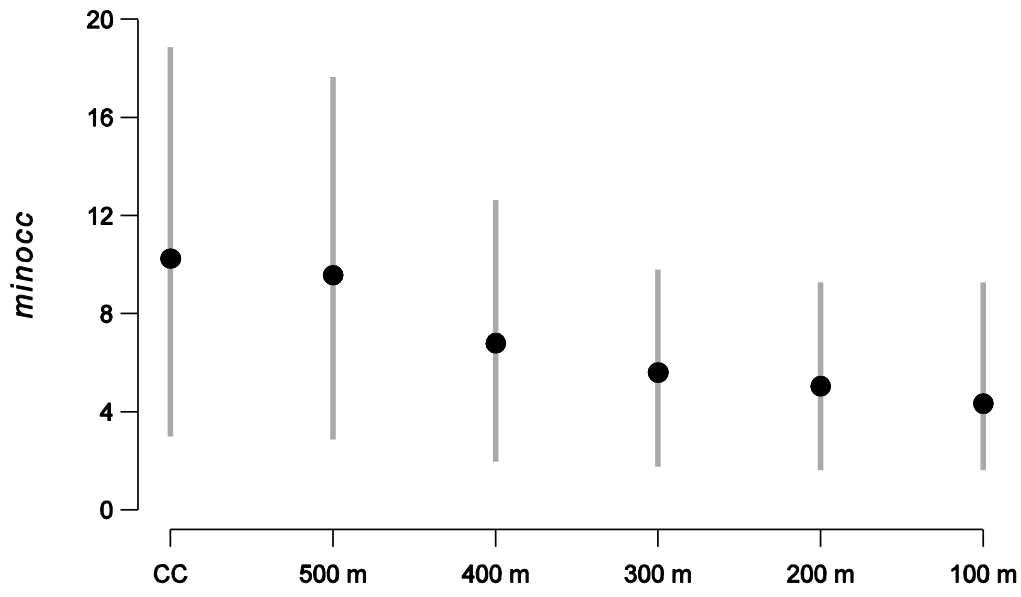
703 **Fig. 4.** Change in the minimum number of occupied wetlands ( $\Delta minocc$ ) and the probability of  
704 quasi-extinction ( $\Delta qe$ ) for the Donnybrook metapopulation of *Litoria raniformis* over 30 years, given  
705 reservation of all land within 200 m of both streams in this area, and the creation of either two, four,  
706 six or eight new wetlands. A score of zero on the y-axis represents no change in  $qe$  or  $minocc$  from  
707 current conditions. Points represent the mean estimates, and vertical lines represent the 95% credible  
708 intervals.



709

710

711 **Fig. 1**



Scenario

712

713

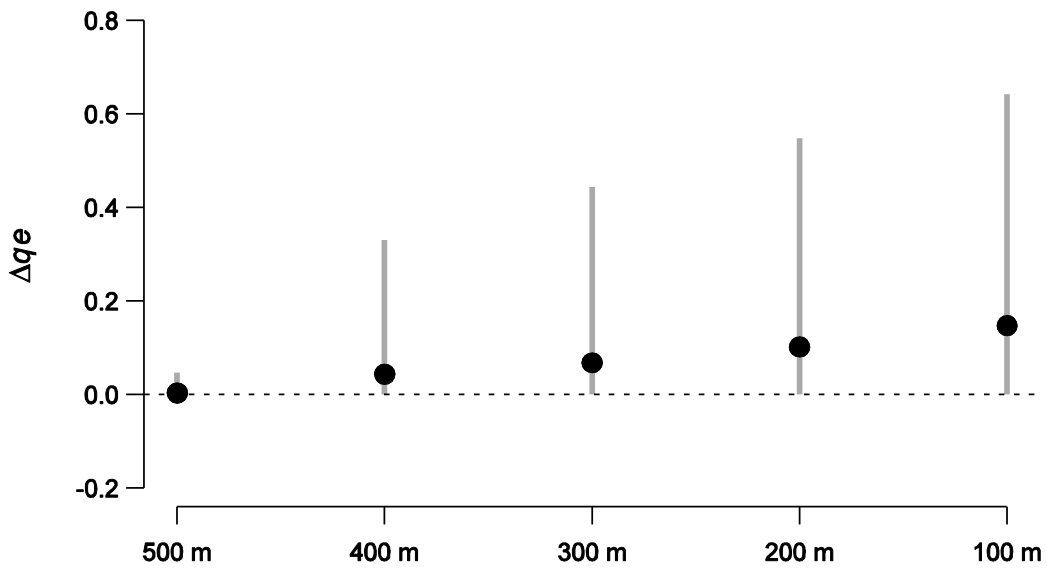
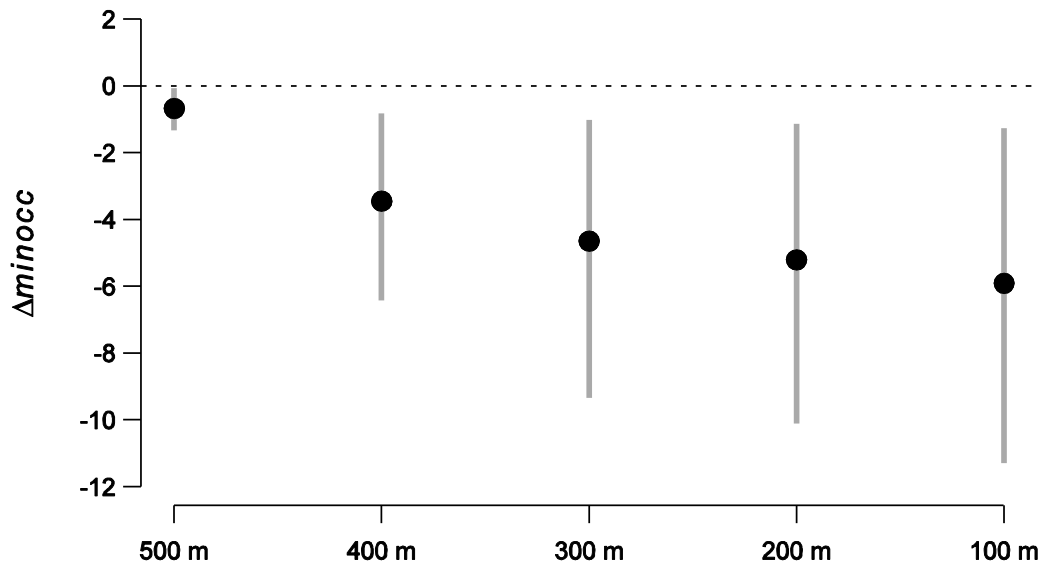
714

715

716

717

718 Fig. 2



Scenario

719

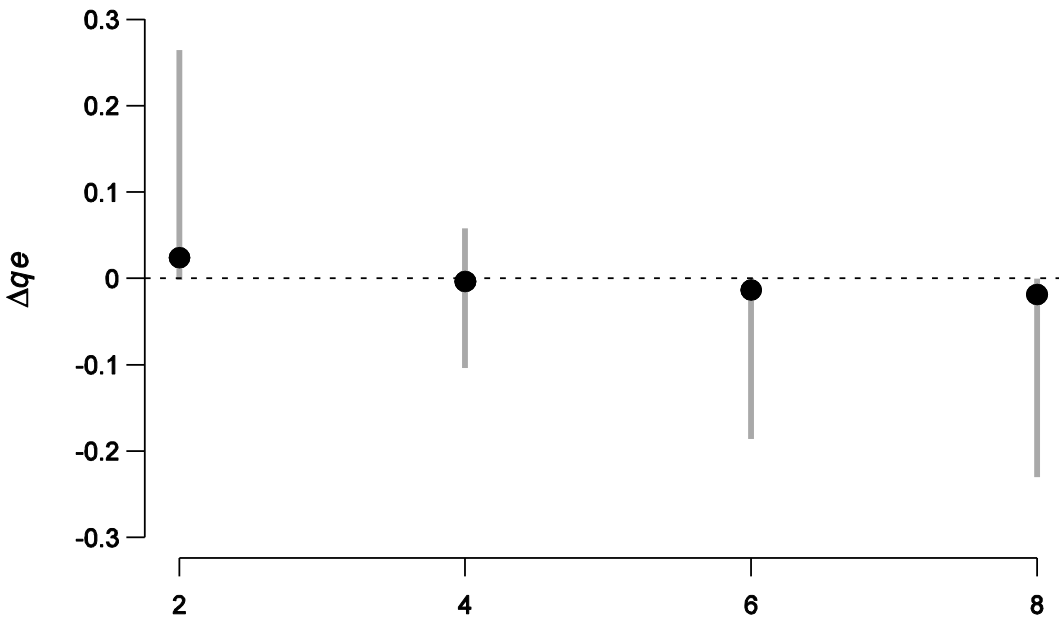
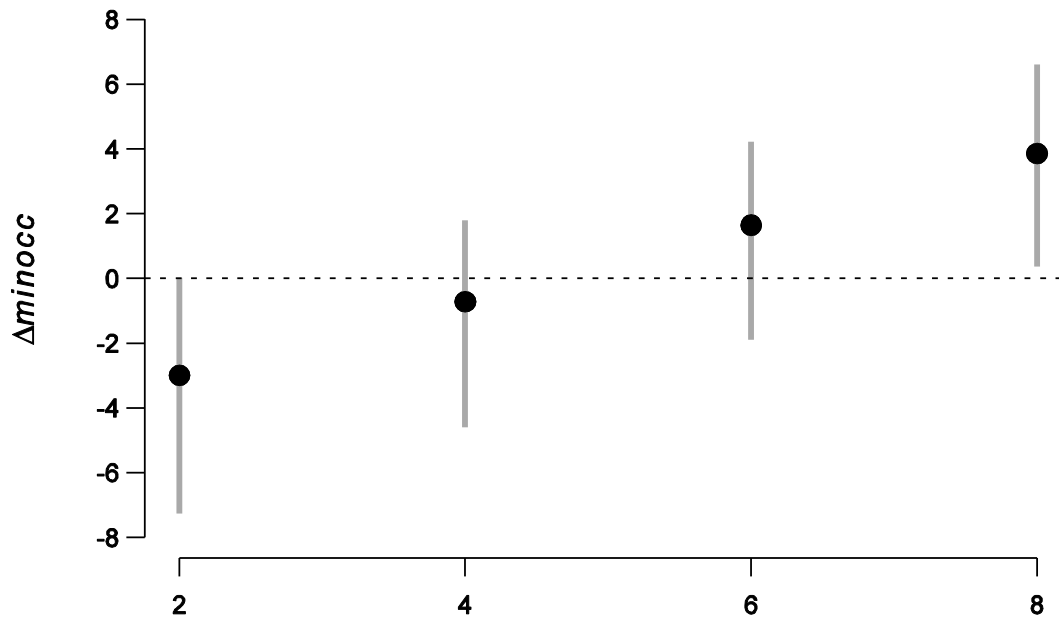
720

721

722

723

724 **Fig. 3**



Number of new wetlands

725

726

727

728

729

730 **Fig. 4**