Modelling habitat management options for the Green and Golden Bell Frog and Growling Grass Frog in the Avon-Perry River area, East Gippsland



Final Report

to

Greening Australia

by

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Michael Scroggie (Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning) developed the optimisation approach used in this project. Michael is thanked for his counsel throughout this project, and his assistance to adapt the approach to this particular case-study. This project could not have been completed without his generosity.

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Cover photos: Created wetland habitat in the Avon-Perry River area, with inserts of the Green and Golden Bell Frog (*Litoria aurea*) and Growling Grass Frog (*Litoria raniformis*). Photos: G. Heard.

1. Introduction

The Green and Golden Bell Frog (*Litoria aurea*) and Growling Grass Frog (*L. raniformis*) were once widely sympatric across East Gippsland in Victoria, as well as higher altitude regions in south-eastern Australia from the Monaro Tablelands to the Central Tablelands west of Sydney (Osborne *et al.* 1996, Hamer *et al.* 2010, Mahony *et al.* 2013). Beginning in the late 1970s, both species declined precipitously in these higher elevation locations, with declines of lowland populations noted through the 1980s and 1990s. These declines occurred simultaneously with a wave of amphibian population declines and extinctions across eastern Australia, known today to be the outcome of the incursion and spread of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) across this region (Scheele *et al.* 2017). Both *L. aurea* and *L. raniformis* are now listed as Vulnerable to Extinction under the Federal *Environment Protection and Biodiversity Conservation Act*, with *L. raniformis* listed as Endangered in Victoria and *L. aurea* listed as Vulnerable (DEPI 2013).

Today, there are just two remaining sites at which *L. aurea* and *L. raniformis* co-occur, both in the central zone of East Gippsland. One is the morass environments and surrounding wetlands in the vicinity of the junction of the Avon and Perry Rivers near Stratford, and the other the Ewing's Morass Wildlife Reserve at which *L. raniformis* has only recently been rediscovered (J. Tscharke, Parks Victoria, pers. comm.). These two remaining sites of sympatry are of considerable conservation value for these species. They represent the remnants of a wide-spread zone of geographic overlap, and therefore represent the last sites at which the ecological and evolutionary dynamics of these closely-related sister-species are ongoing. With the long-held hypothesis that these species hybridise in East Gippsland (Thomson *et al.* 1996), the conservation genetics of these populations is especially interesting. It is plausible that genetic diversity and unique haplotypes occur in East Gippsland, as suggested by the high frequency of unique haplotypes in *L. raniformis* populations in West Gippsland relative to those from the volcanic plains around Melbourne (Keely *et al.* 2015). The preservation of populations within the remaining zone of sympatry should be a national priority for recovery planning for *L. aurea* and *L. raniformis*.

This study is focussed on the conservation of remnant populations of *L. aurea* and *L. raniformis* in the Avon-Perry River area, and specifically habitat management actions that may be applied to meet this objective. The area has been the focus of previous surveys for both species (Collyer 2016), as well as habitat creation and enhancement initiatives that now represent crucial drought refuges and support breeding populations. The current study – commissioned by Greening Australia – sought to assess priorities for extending these initiatives, coupling a patch occupancy model for *L. raniformis* with a recently developed optimisation approach to rank potential habitat creation and enhancement options for both species. The aim of these analyses was to identify a set of habitat management options that represented the best combination for maximising metapopulation viability of these frogs in the Avon-Perry River area.

2. Methods

Field sites and habitat assessments

This study focussed on 54 sites in an area bounded roughly by the Avon River in the south, Bengworden Rd in the west, Stratford-Bengworden Rd in the north and Perry River in the east (Figure 1).

The area is characteristic of grazing land in the Gippsland Lakes, being dominated by cleared pasture land, but with either significant remnant wetlands or farm dams that support wetland species to varying degrees. Within and adjoining the study area, major wetland environments are provided by the Clydebank Morass and associated wetlands at the head of Lake Wellington. These sites display highly dynamic water-levels and salinity. While often uninhabitable due to very high salinity (at or above that of seawater), these sites can provide extensive habitat for *L. aurea* and *L. raniformis* in wet years, when salinity drops substantially and large breeding aggregations have been recorded (M. Potts, Greening Australia, pers. comm.; G. Heard pers. obs.). However, core habitat for the species are mostly smaller wetlands, including spring-soaks constructed specifically for these frogs (see cover image), livestock dams and small, remnant swamps.

All potential wetland habitat for *L. aurea* and *L. raniformis* in and immediately adjacent to the study area was mapped with the aid of Google Earth, including morass environments, livestock dams and constructed spring-soaks. Habitat assessments were completed at these sites in March 2020, focussing on the primary characteristics known to influence the occupancy dynamics of *L. aurea* and *L. raniformis* (Table 1), and which were required for applying the existing model of patch occupancy dynamics of *L. raniformis* to the problem of prioritising habitat management options for the species. Initial habitat assessments were undertaken by the author in collaboration with M. Potts, and subsequently completed by the latter. Initial collaborative assessments sought to ensure equivalence in visual estimates of aquatic and riparian vegetation cover during assessments at which the author was not present. Site photos were also taken for this purpose, allowing post-hoc assessment of vegetation cover estimates to ensure the observer bias was minimised.

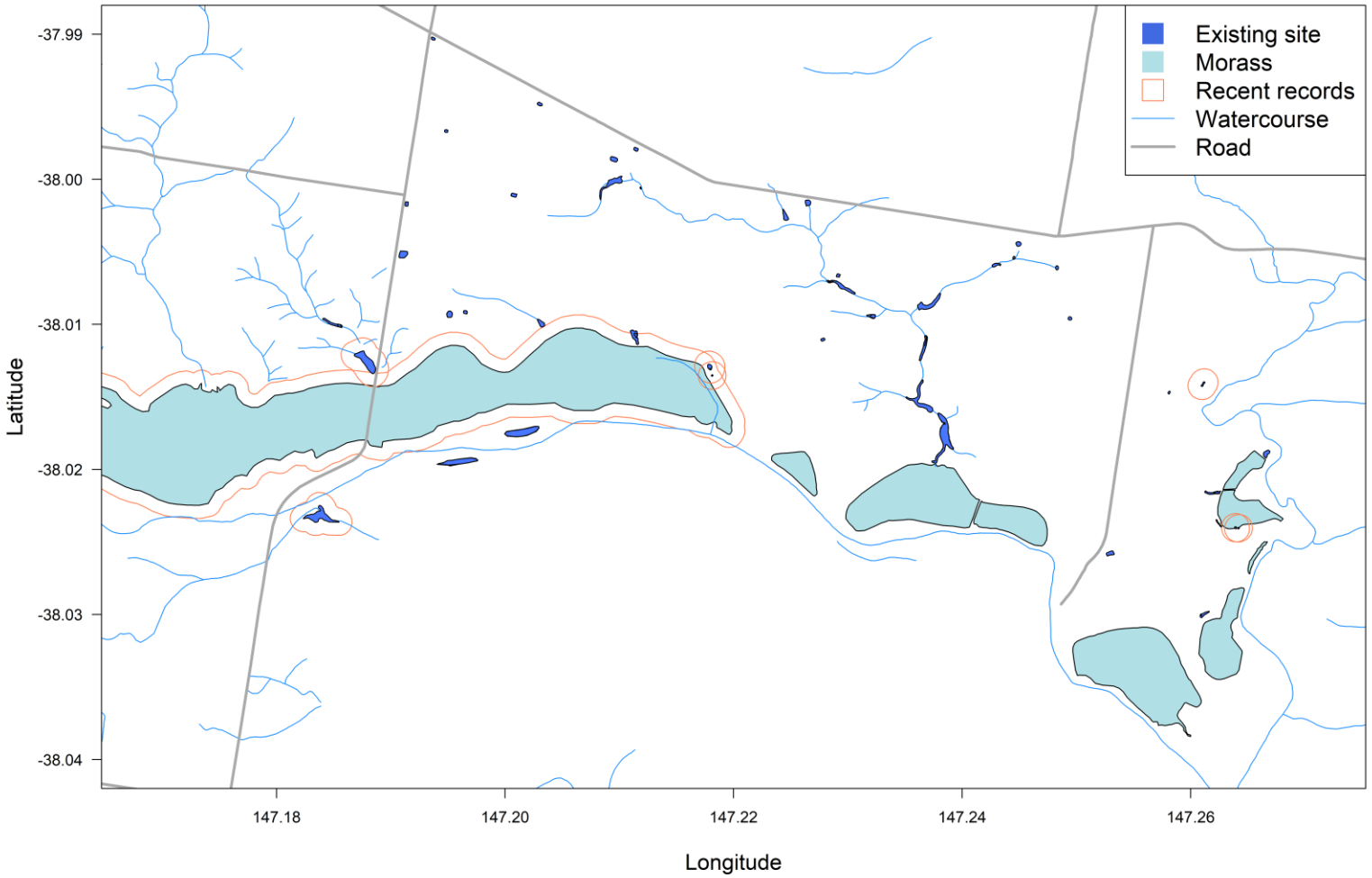


Figure 1. Map of the study area, showing existing potential habitat for the Green and Golden Bell Frog (*Litoria aurea*) and Growling Grass Frog (*L. raniformis*), as well as morass environments that provide habitat when inundated and salinity is low. Sites with recent records of either species are highlighted by an orange buffer.

Table 1. Key variables influencing the occupancy dynamics of the Green and Golden Bell Frog (*Litoria aurea*) and Growling Grass Frog (*L. raniformis*).

Variable	Sub-categories	Metric	Influences	References
Site size	Surface area	m^2	Persistence	5, 11
	Maximum depth	cm		
Permanence	Intermittent	-	Persistence & colonisation	2, 5, 8, 12
	Ephemeral			
	Semi-permanent			
	Permanent			
Elevation	-	m asl	Persistence	4, 9, 11
Aquatic vegetation cover	Emergent vegetation	%	Persistence	1, 3,8, 13
	Submergent vegetation			
	Floating vegetation			
Shading vegetation cover	Trees	%	Persistence	11
	Shrubs			
	Emergent vegetation			
Salinity	Conductivity	(µS/cm)	Persistence	7, 10, 11, 14
Edge-to-edge distance between sites	-	km	Colonisation	1, 2, 5, 6, 8, 11, 12

1, Hamer *et al.* (2002); 2, Hamer *et al.* (2008); 3, Heard *et al.* (2008); 4, Hamer *et al.* (2010); 5, Hamer and Mahony (2010); 6, Heard *et al.* (2012); 7, Stockwell *et al.* (2012); 8, Heard *et al.* (2013); 9, Mahony *et al.* (2013); 10, Heard *et al.* (2014); 11, Heard *et al.* (2015); 12, Valdez *et al.* (2015); 13, Valdez *et al.* (2017); 14, Clulow *et al.* (2018).

Habitat management options

Potential enhancements to existing sites and opportunities for further habitat creation in the study area for *L. aurea* and *L. raniformis* were identified during a half-day workshop with M. Potts. We systematically reviewed each of the 54 existing sites to determine the practicality of habitat enhancement works that aimed to increase site suitability for *L. aurea* and *L. raniformis*, with specific focus on the variables listed in Table 1. As such, we assessed the capacity to increase the size and depth of existing sites, increase their aquatic vegetation cover and reduce their shading vegetation cover. We considered site salinity to be unmanageable in this system beyond previous works that have been implemented to close sources of salt influx into morasses and aid flushing of salts from these sites in high rainfall years. In total, we identified 18 sites at which enhancements could be pursued and specified practical targets for each variable at each of these sites.

To complement potential habitat enhancement initiatives, we mapped two potential new wetlands to be constructed for *L. raniformis* and *L. aurea* in the study area. Both of these sites were located in areas judged to either have sufficient catchment areas to ensure the resulting wetlands were permanent or semi-permanent, or where permanent springs with adequate seepage

rates were known to occur. Sites identified for potential habitat enhancements or wetland creation are shown in Figure 2 and detailed in Appendix 1.

Patch occupancy model

Modelling framework

This study used an existing patch occupancy model for *L. raniformis* developed from long-term monitoring data collected north of Melbourne (Heard *et al.* 2012, 2013, 2015, Rose *et al.* 2016) to critique habitat enhancement or creation options for this species and *L. aurea* in the study area. Patch occupancy models focus solely on the extinction and colonisation dynamics of species within habitat networks and are built from functions that describe relationships between the annual probabilities of population persistence and colonisation and features of both the patches themselves and their topology (for example, patch size, habitat quality and connectivity; MacKenzie *et al.* 2006). These models are useful for species that display considerable turnover in patch occupancy, and for which the internal demographic rates are difficult to estimate. Patch occupancy models have become popular among amphibian ecologists for these reasons, particularly those studying wetland-breeding frogs.

Like other metapopulation models, patch occupancy models also allow the viability of population networks to be estimated through simulation (Hanski 1999, Morris and Doak 2002, Nicholson and Ovaskainen 2009). Starting from a known, guessed or random pattern of occupancy within a habitat network, simulation of occupancy dynamics from one time-step to the next proceeds by estimating the probability of persistence at all currently occupied patches (using the relationships between this probability and patch characteristics) and estimating the probability of colonisation of all currently vacant patches (typically using relationships between this probability and connectivity to neighbouring occupied patches). Actual extinction or colonisation at each time-step is a random event occurring at a rate set by these probabilities, with fluctuating occupancy in the network monitored through time. Such simulations may be run thousands of times, allowing estimates of viability metrics such as the probability of metapopulation extinction or the average minimum occupancy across simulations.

I used this modelling approach, coupled with an optimisation algorithm (see below), to assess the alternative habitat management options in the study area. Specifically, I sought to rank these various options based on their contribution to metapopulation viability for *L. raniformis*, making the explicit assumption that this ranking would be equivalent for *L. aurea*, due to the similar ecology, habitat affiliations and dispersal distances of these species (Table 1), and the fact that they often occupy the same sites in the study area (M. Potts pers. comm.; G. Heard pers. obs.), as they did historically where sympatric (Humphries 1979, Osborne *et al.* 1996, Mahony *et al.* 2013).

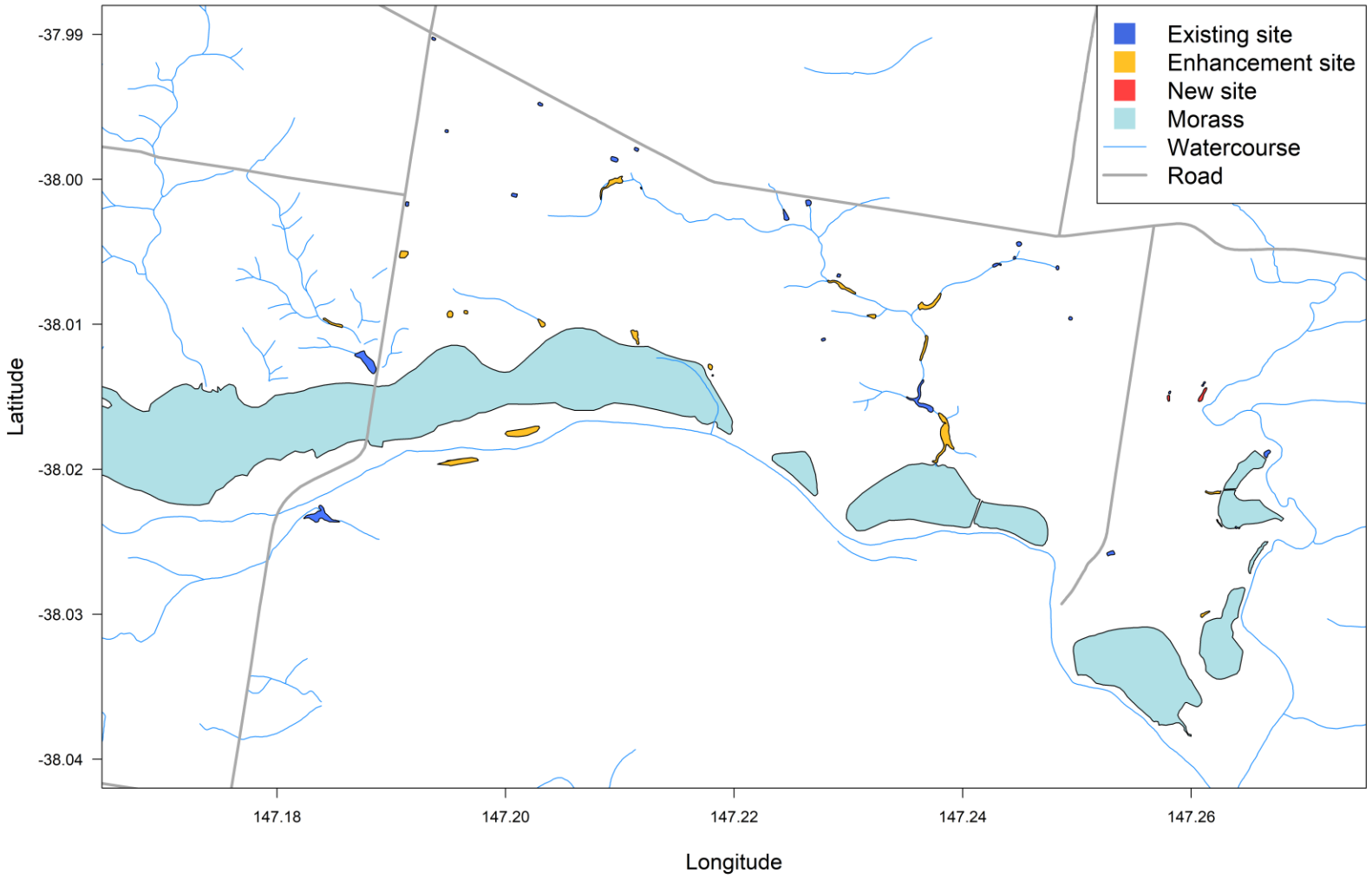


Figure 2. The distribution of potential management options considered for the Green and Golden Bell Frog (*Litoria aurea*) and Growling Grass Frog (*L. raniformis*) in the study area, including the 18 sites at which habitat enhancement was considered feasible and the two new sites that could be constructed.

The occupancy model

The occupancy model used in this study is an extension of that of Heard *et al.* (2013, 2015) and Rose *et al.* (2016). The model was developed using additional data from the long-term monitoring project from which these earlier studies derived (G. Heard *et al.*, unpublished) and includes effects of additional variables.

The model was parameterised using 16 years of monitoring data for *L. raniformis* across northern Melbourne using the approach of Mackenzie *et al.* (2003, 2006). This approach uses monitoring data from a set of sites acquired over multiple years, with repeat surveys completed within years, to jointly estimate four fundamental parameters: the probability of occupancy in the first season (ψ), the annual probability of persistence at occupied sites (ϕ), the annual probability of colonisation of vacant sites (γ) and the per-survey probability of detection (p). The approach is highly flexible, allowing each of these parameters to be modelled as functions of variables hypothesised to influence them, such as site characteristics for the occupancy parameters and survey-level variables for the probability of detection. Typically, these relationships are modelled using logistic regression. For example, effects of patch characteristics on the probability of persistence are modelled as:

$$\log\left(\frac{\phi_i}{1-\phi_i}\right) = \alpha + \beta_1 \cdot \left(X_{1,i}\right) + \beta_2 \cdot \left(X_{2,i}\right) + \ldots + \beta_n \cdot \left(X_{n,i}\right), \qquad \text{(Eq. 1)}$$

where α is the intercept, $X_{1,i \to n,i}$ are the relevant variables and $\beta_1 \to \beta_n$ are regression coefficients.

The model was fitted to the data using Markov Chain Monte Carlo (MCMC) sampling with the aid of the software package `MultiBUGS` (Goudie *et al.* 2020a) called from `R` (R Core Team 2021) with the aid of the `R2MultiBUGS` package (Goudie *et al.* 2020b). The annual probability of population persistence (ϕ) was modelled as a function of site size (as log(site surface area × maximum depth)), site elevation, aquatic vegetation cover, shading vegetation cover and site salinity. The annual probability of colonisation of vacant sites (γ) modelled as a function the cumulative probability of immigration from neighbouring sites within 2 km. The posterior distributions of the effects of these variables on the probabilities of population persistence and colonisation are provided in Table 2, with estimated relationships shown in Figure 3.

Site surface area (m^2) was defined as the area covered at the upper water-level and maximum depth (cm) estimated visually. Site size estimated in this way is a predictor of wetland microclimate and the resulting prevalence of chytrid infections, with larger, deeper wetlands being warmer across the active season and displaying lower rates of chytrid infections as a result (Heard *et al.* 2015). Site elevation (metres above sea level) is also an important predictor of wetland microclimate, with water temperatures during the active season being lower at higher elevation sites.

Table 2. Summary statistics for the patch occupancy model for the Growling Grass Frog (*L. raniformis*) used in this study to prioritise habitat management options within the study area.

Parameter	Effect of	Mean	SD	Lower 95% CI	Upper 95% CI
Probability of colonisation	Intercept	-4.157	0.375	-5.004	-3.503
Probability of colonisation	Connectivity	6.597	1.295	4.655	9.902
Probability of persistence	Intercept	1.122	0.191	0.744	1.511
Probability of persistence	Site size	1.315	0.389	0.579	2.129
Probability of persistence	Aquatic vegetation cover	3.202	0.639	2.058	4.528
Probability of persistence	Shading vegetation cover	-1.364	0.534	-2.447	-0.339
Probability of persistence	Salinity	0.782	0.341	0.100	1.479
Probability of persistence	Elevation	-0.834	0.320	-1.478	-0.180

As such, chytrid infection rates are higher at higher elevation sites (Heard *et al.* 2015). Following Heard *et al.* (2013) and Rose *et al.* (2016), aquatic vegetation cover was defined as a simple index that seeks to balance cover and structural diversity. It was the average of emergent, submerged and floating vegetation cover in the wetland. Shading vegetation cover was defined as the average cover of trees and shrubs on the bank and emergent vegetation within the wetland. Wetlands with higher cover of these vegetation types are cooler on average and therefore display higher rates of chytrid infections across the active season (Heard *et al.* 2015). Finally, chytrid infection rates fall with increasing salinity, due to the intolerance of the waterborne zoospores of the fungus to higher salinity (Stockwell *et al.* 2012, Heard *et al.* 2014, Heard *et al.* 2015, Clulow *et al.* 2018). It was defined as the natural logarithm of electrical conductivity (μS/cm).

As above, the annual probability of colonisation of vacant sites was modelled as a function of the estimated cumulative probability of immigration from neighbouring sites within 2 km (a measure of site 'connectivity'). The underlying logic is that the likelihood of a site being successfully colonised by the species should scale with the number of migrants it receives, which it turn relates to the number of neighbouring sites that are occupied (and can therefore be sources of migrants) and the probability of dispersal from these neighbouring sites to the focal site. Following Chandler *et al.* (2015), I elected to use the cumulative probability of immigration (*I*) from neighbouring sites as a useful index of migration rate, calculated as:

$$I_i = 1 - \prod_{j=1}^{N} \left(1 - \left(o_j \cdot d_{j,i}\right)\right), \qquad \text{(Eq. 2)}$$

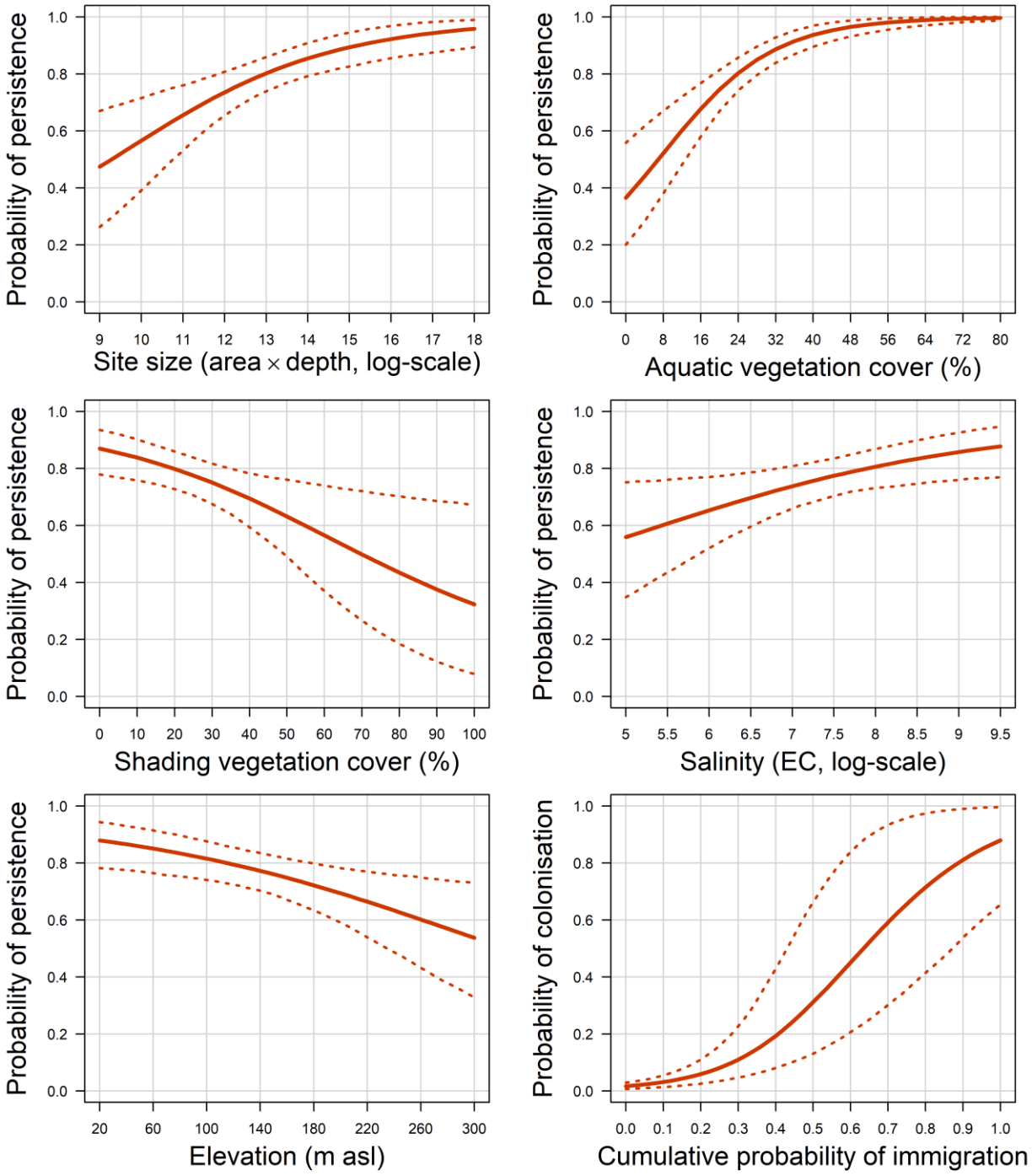


Figure 3. Estimated relationships between wetland- and landscape-level covariates and the annual probabilities of population persistence and colonisation for the Growling Grass Frog (*Litoria raniformis*). Mean estimates are shown (solid lines) along with the 95% credible interval (dashed lines).

where I_i is the cumulative probability of immigration to site i, o_j is the occupancy probability of neighbour j and $d_{j,i}$ is the probability of dispersal from neighbour j to site i. The probability of dispersal to site i from each neighbouring site j ($d_{j,i}$) was estimated as:

$$\log\left(\frac{d_{j,i}}{1-d_{j,i}}\right) = 0.006 - 2.991 \cdot dist_{j,i}, \qquad \text{(Eq. 3)}$$

where $dist_{j,i}$ is the minimum straight-line, edge-to-edge distance between neighbour j and site i (in km). This function (depicted in Figure 4) was estimated from the long-term monitoring data, with mark-recapture data from a subset of sites (Heard *et al.* 2012) used to develop prior estimates of the intercept and distance effect.

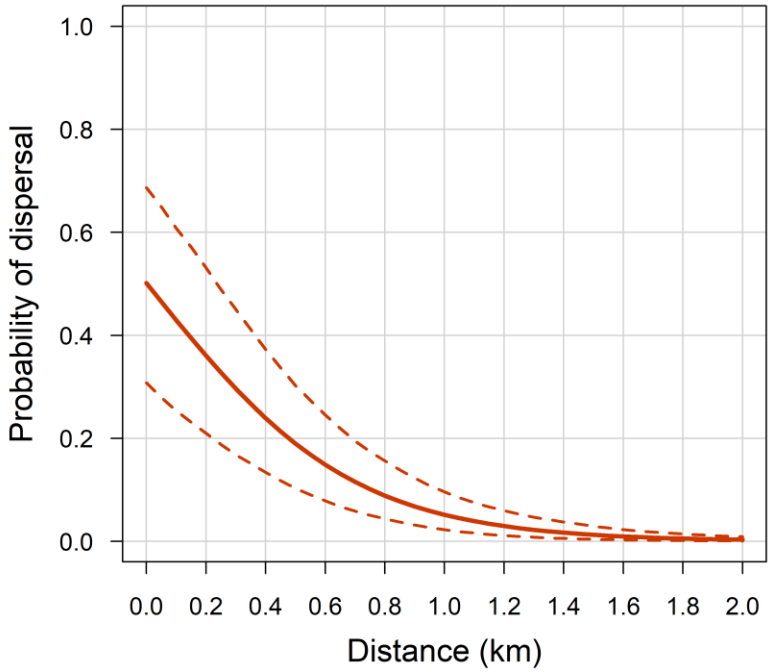


Figure 4. Dispersal function for Growling Grass Frog (*Litoria raniformis*) used to estimate the probability of dispersal between neighbouring sites, and hence, site connectivity. While this function was developed from data on *L. raniformis* only, *L. aurea* is known to display a similar dispersal kernel with few movements greater than 2 km (Hamer *et al.* 2008).

Prioritisation of habitat management options

Scroggie *et al.* (2019) designed an optimisation algorithm to prioritise wetland construction initiatives for *L. raniformis* in Melbourne's urban growth areas, using simulations from the patch occupancy model of Heard *et al.* (2013) to test alternate sets of sites to build with regard to their

contribution to metapopulation viability. The approach is a modified simulated annealing algorithm (Kirkpatrick *et al.* 1983) that tests alternative sets of wetlands to build within a predefined budget. Briefly, the algorithm iteratively steps through alternative sets of sites by: (i) selecting a set of potential sites to construct within the budget in a semi-random fashion; (ii) testing the value of this set by running a metapopulation viability analysis for that set and existing sites using a patch occupancy model, and; (iii) recording the viability metric derived from the simulations for that set. After a pre-defined number of iterations, the algorithm returns the set of sites that gave the highest metapopulation viability – the optimal solution (of those trialled).

While Scroggie *et al.* (2019) focussed on identifying the optimal set of wetlands to construct for *L. raniformis*, the approach may be adapted to consider both wetland construction and enhancement actions. I collaborated with M. Scroggie (Arthur Rylah Institute for Environmental Research, Victorian Department of Environment, Land, Water and Planning) to implement this adaption, as well as adjusting the metapopulation simulations used by the algorithm to take wetland filling and drying regimes of all sites into account, plus allow for rainfall-driven fluctuations in the salinity (and hence, habitability) of morasses in the simulations.

Data

I began by collating each element of data required to run metapopulation simulations within the study area. This included the variables that explicitly determine the probabilities of population persistence and colonisation within the patch occupancy model, as well as other variables that were used to simulate the hydrological dynamics of all sites and fluctuations in salinity in morass environments.

For existing sites, maximum depth, aquatic vegetation cover, shading vegetation cover and salinity were all available from the habitat assessments conducted for this study. Their surface area was extracted from mapping completed in Google Earth, as was their elevation. For each habitat enhancement option identified, we designated how each of these habitat variables would change, either increasing or decreasing to improve habitat quality (Appendix 1). As such, I simply collated these data to define the altered characteristics of each enhancement site. For proposed wetlands to be added to the system, surface areas were extracted from mapping of their potential extent and all other variables designated *a priori* with a view of maximising their habitat quality (Appendix 1). Straight-line, edge-to-edge distances between all sites (existing unenhanced, existing enhanced and proposed sites) were calculated with the aid of the `sf` package (Pebesma 2018) in `R` using site polygons mapped in Google Earth.

Annual rainfall data for Stratford (10 km NNE of the study area) from 1969 onwards was extracted from the Australian Bureau of Meteorology's 'Climate Data Online' portal (http://www.bom.gov.au/climate/data/), with 1969 being the first full year of recording at that station. As described below (see *'Metapopulation simulations'*), these data were used to define

rainfall variability in the study area and simulate both wetland filling and drying regimes, and fluctuations in the salinity of morass environments. Simulations of wetland filling and drying also relied on designations of site 'permanence'; an ordinal score of the likelihood of a site holding water in any given year based on their susceptibility to rainfall variability (Table 1). These permanence scores were: 1 = 'intermittent' (fills rarely, during high rainfall years only); 2 = 'ephemeral' (fills most years during winter and spring, but dries over summer); 3 = 'semi-permanent' (dries out occasionally during low rainfall years), and; 4 = 'permanent' (never dries out fully, regardless of rainfall variability). Designations of site permanence for existing sites were made in the field based on water source, depth and vegetation characteristics, and checked using historical imagery of the study area accessed through Google Earth. Of those sites at which enhancements were proposed, site permanence was increased to semi-permanent or permanent based on proposed changes to their size (surface area and depth). Proposed new sites were set to be permanent.

Metapopulation simulations

For any given set of management options (habitat enhancements or creation) selected by the optimisation algorithm, simulations of metapopulation dynamics were run including the wetlands selected, plus all other wetlands in the study area. Occupancy dynamics were simulated forward for a period of 30 years in each case, with occupancy tracked for calculating metapopulation trajectories.

Fundamental to this was simulating whether each site held water in each year, with occupancy of each site only allowed in those years they held water (in line with the highly aquatic nature of *L. aurea* and *L. raniformis*; Heard *et al.* 2008, Wassens *et al.* 2008, Valdez *et al.* 2016, Valdez *et al.* 2017). In each year, whether sites held water or not was defined by a model of wetland hydrology developed from the long-term monitoring of *L. raniformis* around Melbourne. In that dataset, all monitoring sites have received the same permanence score as described above. In addition, sites have been scored as 'inundated' (1) or 'dry' (0) in each year when monitoring has occurred, with scoring in years when monitoring did not take place achieved with the aid of historical imagery in Google Earth. The resulting matrix of inundation scores allowed a hierarchical logistic regression model to be fitted, with predictors being a site's permanence and rainfall in the 12 months up to the end of the active season in May (hence, encompassing the active season itself [September–May] and the preceding winter). Separate effects of rainfall were included for each permanence score, allowing the relationship between rainfall and the probability of inundation that the permanence scores were originally devised to capture to be estimated from the data. The model was structured as:

$$\log\left(\frac{\lambda_{i,t}}{1-\lambda_{i,t}}\right) = \alpha_{perm[i]} + \beta_{perm[i]} \cdot rainfall_t \,, \qquad \text{(Eq. 4)}$$

where $\lambda_{i,t}$ is the probability of site *i* being inundated in year *t*, α is the intercept which varies according to the permanence (*perm*) of site *i* and β is the regression coefficient for the effect of rainfall in year *t* on inundation probability of site *i*, also dependent on its permanence score. Posterior estimates of the parameters of this model are provided in Table 3, with relationships between the probability of inundation, annual rainfall and site permanence depicted in Figure 5.

Table 3. Summary statistics for the model of the probability of site inundation in each year, used in the simulations to allow wetlands to fill and dry with fluctuations in rainfall.

Parameter	Permanence category	Mean	SD	Lower 95% CI	Upper 95% CI
Intercept	Intermittent	-0.243	0.282	-0.788	0.319
Intercept	Ephemeral	1.538	0.200	1.172	1.958
Intercept	Semi-permanent	3.090	0.210	2.693	3.514
Intercept	Permanent	18.644	14.986	7.992	56.160
Rainfall effect	Intermittent	3.391	0.776	2.087	5.047
Rainfall effect	Ephemeral	3.173	0.540	2.210	4.306
Rainfall effect	Semi-permanent	2.105	0.544	1.046	3.157
Rainfall effect	Permanent	2.535	3.485	-5.718	8.824

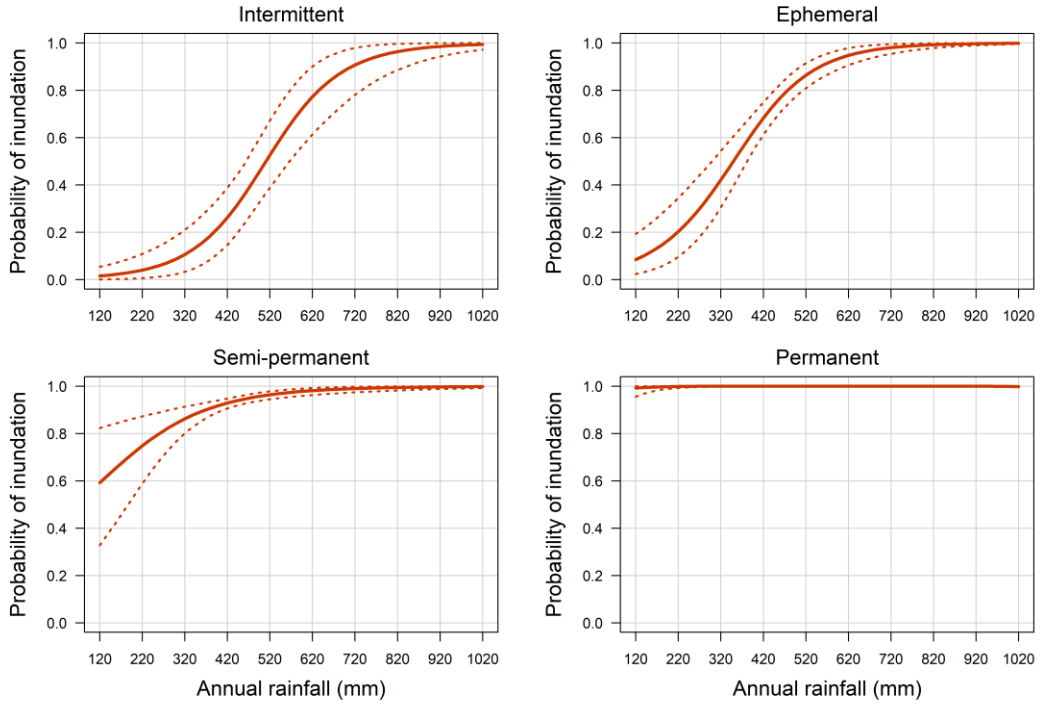


Figure 5. Relationships between annual rainfall (in millimetres) and the probability of inundation for wetlands in the four permanence categories. These relationships were used in the simulations to allow wetlands to fill and dry with fluctuations in rainfall.

In each year of each simulation run, I set rainfall from June to May to be a random draw from a normal distribution with a mean and standard deviation for this 12-month window taken from the Stratford rainfall data. In each year, the probability of inundation of each site was estimated as per Equation 4, and actual inundation or not of each site set as a Bernoulli trial with this probability. This approach allowed for temporally-correlated filling and drying events, based on annual rainfall fluctuation. However, it required assuming that the relationships between the probability of inundation, site permanence and rainfall estimated from Melbourne hold for the study area.

Rainfall simulations were also used to allow morass sites to be habitable during high rainfall years, reflecting the observed dynamics in the study area. I defined saline sites as those with electrical conductivity >15,000 μS/cm at the time of habitat assessments in March 2020 (Appendix 1). In each simulation run, these sites were set to only be habitable in years when rainfall was at, or above, the 90th percentile for Stratford (782 mm). In these years, salinity was reset to 5,000 μS/cm, in line with salinity readings from Lake Wellington during the 2011/2012 La Niña period.

Occupancy simulations started from an assignment of initial occupancy at each site based on recent observations. Only eight sites are known to have been occupied in the last two years, meaning that the simulations began with occupancy of these refuge sites in all cases.

For each year subsequent to the first, simulation of occupancy dynamics proceeded by: (i) estimating the probability of occupancy for each site at the next time-step ($O_{i,t+1}$), according to their occupancy status in the previous time step and site-specific probabilities of population persistence and colonisation (as defined by site size, elevation, aquatic vegetation cover, shading vegetation cover, salinity and connectivity; see equation 5); (ii) setting occupancy of each site at the next time-step as the outcome of a Bernoulli trial with probability $O_{i,t+1}$, and; (iii) recording the occupancy status of each site at the next time-step. In order to incorporate uncertainty in the parameters of the persistence and colonisation functions, each simulation run was completed using a new random set of parameter estimates derived during model fitting. For further details on the approach, see Heard *et al.* (2013). The fundamental equation for simulating the occupancy dynamics of each site *i* from one year to the next is as follows:

$$O_{i,t+1} = o_{i,t} \cdot \phi_i + (1 - o_{i,t}) \cdot \gamma_{i,t}, \qquad \text{(Eq. 5)}$$

where $O_{i,t+1}$ is the probability of occupancy of site *i* at time *t*+1, $o_{i,t}$ is the occupancy status of site *i* at time *t* (1 if occupied, 0 otherwise), and ϕ_i and $\gamma_{i,t}$ are the probabilities of persistence and colonisation for site *i* at time *t* (MacKenzie *et al.* 2006).

Prioritisation approach

The optimisation algorithm of Scroggie *et al.* (2019) was designed to find a single optimal solution to the question of which wetlands to construct to support *L. raniformis* metapopulations.

However, to acknowledge that this solution may change dependent on the parameters of the underlying metapopulation model, I opted to pursue a prioritisation of habitat management initiatives in the Avon-Perry River study area, where the prioritisation is the frequency each site is selected by the optimisation algorithm when it uses different combinations of estimates of parameters of the metapopulation model, drawn from their posterior distributions (Table 2).

To do so, the optimisation was run 100 times, each time using a randomly-chosen set of estimates of the parameters of the metapopulation model. The optimal solution after 50 iterations of the algorithm was recorded for each run, recalling that at each iteration, the algorithm selects a new set of enhancement or creation options to trial and applies metapopulation simulations to test this selection. I ran 100 metapopulation simulations per iteration of the algorithm. The budget of enhancement or creation initiatives was nominally set at 12 for each iteration, representing 60% of those possible. Each optimal solution from the 100 runs consisted of the selection or non-selection of the 20 potential habitat management options (denoted by a 1 or 0 respectively), allowing calculation of the proportion of runs in which each option was included in the optimal set. This proportion was used as the metric of a sites' priority.

The objective of the prioritisation analysis was to maximise minimum occupancy across the entire metapopulation across the course of the 30-year simulation period. Minimum occupancy is a measure of the contribution of a set of habitat management options to occupancy of the broader metapopulation, and resulting estimates of the priority of habitat management options with this objective represents the extent to which they help reduce stochastic falls in occupancy across the simulation period, and therefore, reduce metapopulation extinction risk. Minimum occupancy was recorded for each of the 100 simulations run at each iteration of the optimisation algorithm, with the mean across simulations used as the viability metric for each iteration.

With 100 runs of the optimisation, during which the algorithm completed 50 iterations of site selections and simulated the occupancy dynamics 100 times for each selection, the computational burden was significant. The analysis was completed in `R` using parallel processing to speed up computations. Parallel processing was achieved with the aid of the `future` and `future.apply` packages (Bengtsson 2020).

Results

Selection frequencies for each of the 20 sites considered in the prioritisation are shown in Figure 6, with rankings of site priority mapped in Figure 7. Full site details are provided in Appendix 2.

The two habitat creation options – sites 52 and 53 – were clear top priorities. Site 52 was included in the optimal set on 100% of occasions, and site 53 included on 99% of occasions. These sites are located close to two existing spring-fed soaks in the north-east of the study area, one of which (that closest to site 52) is known to be currently occupied by *L. aurea* (M. Potts, G. Heard pers. obs.; Figure 1). These sites have the benefit of creating a small metapopulation around the existing spring soaks, and bolstering the size of the overall habitat network.

Enhancing site 3 in the south-east of the study area ranked third in the prioritisation, and has the potential to create an important refuge habitat in this area, close to three morass sites that are potentially suitable breeding habitat in high rainfall years. Sites 35 and 27 represent sites at which significant increases in habitat quality are possible (Appendix 1 & 2). Sites 35, 55 and 36 (ranked 4th, 6th and 7th, respectively) are all located adjacent to the large morass in the south and south-west of the study area and represent potential refuge site during low rainfall years, when this site both has the possibility of drying out or becoming hypersaline.

Enhancements of sites 27 and 26 (ranked 5th and 9th, respectively) of the scale simulated here has the potential to create resilient local populations in the gully that runs roughly north-south through the centre of the study area. Their high rankings suggest that these enhancements could significantly increase connectivity through this central section of the study area, with resulting increases in the resilience of the broader metapopulation to stochastic falls in occupancy through time.

Enhancement of sites 51 (ranked 8th) and 38 (ranked 10th) could secure occupancy of the western edge of the study area. Currently occupied habitat in this area includes the large south-western morass, and two sites adjacent to Bengworden Road (Figure 1). However, as above, the morass is susceptible to drying and hypersaline events. Enhancement of sites 51 and 38 are therefore likely to reduce the risk of extinction at the western edge of the study area, and provide refuges for recolonisation of the morass in high rainfall years.

At the opposite end of the rankings were sites 48, 17, 20, 37 and 7 (placing 16th to 20th, respectively). The last four of these sites already display relatively high habitat suitability for *L. aurea* and *L. raniformis*, being permanent or semi-permanent, large and deep in some cases or with suitable vegetation communities (Appendix 1 & 2). The low ranking of these sites is indicative of this; the gains to minimum occupancy from enhancing these sites was comparatively low in the simulations. Site 48 is currently quite saline (~19,000 µS/cm), meaning that it was only occupiable in the simulations in high rainfall years. The low ranking of site 48 is reflective of this constraint on its contribution to occupancy dynamics.

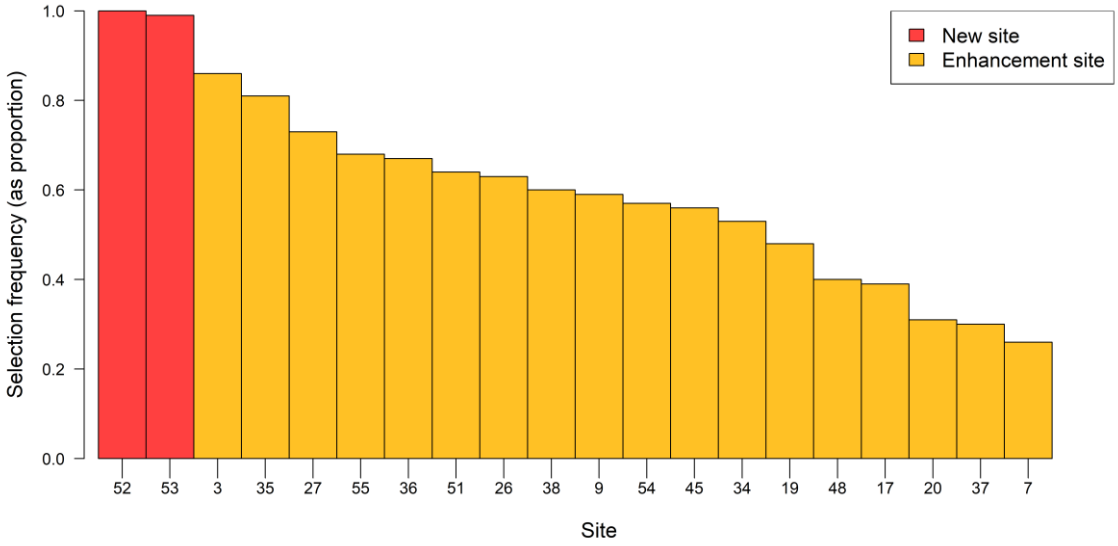


Figure 6. Selection frequency for each of the 20 management options for the Green and Golden Bell Frog (*Litoria aurea*) and Growling Grass Frog (*L. raniformis*) in the study area, where options are either to create a new site or enhance an existing site. Selection frequency is the proportion of runs of the optimisation algorithm in which each site featured in the optimal solution. Sites are depicted spatially in Figure 7.

Discussion

This study sought to prioritise habitat management options for the Green and Golden Bell Frog (*L. aurea*) and Growling Grass Frog (*L. raniformis*) in one of the last remaining areas in south-eastern Australia where these species remain in sympatry – the Avon-Perry River region of East Gippsland. A patch occupancy model developed for *L. raniformis* (Heard *et al.* 2013, Heard *et al.* 2015, Rose *et al.* 2016, G. Heard *et al.*, unpublished) was used for this purpose, coupled with an optimisation algorithm developed previously for prioritising habitat construction initiatives for this species. Both the patch occupancy model and optimisation algorithm were customised for this study, allowing: (i) habitat creation and enhancement options to be assessed simultaneously; (ii) wetland filling and drying regimes to be simulated dependent on rainfall variability, and; (iii) fluctuating salinity (and hence, habitability) of morass sites with rainfall to be simulated to replicate the dynamic contribution of these sites to the metapopulation dynamics of *L. aurea* and *L. raniformis*.

The analysis identified clear priorities from the 20 habitat creation and enhancement tested. Both potentially new sites ranked highest, and should therefore be the primary targets for habitat works in the coming years. Enhancement of sites 3, 35 and 27 (Figure 7) should also be high priorities. Not only were these sites ranked 3rd – 5th, they were selected by the optimisation algorithm on >70% of runs – at least 5% more than any other options.

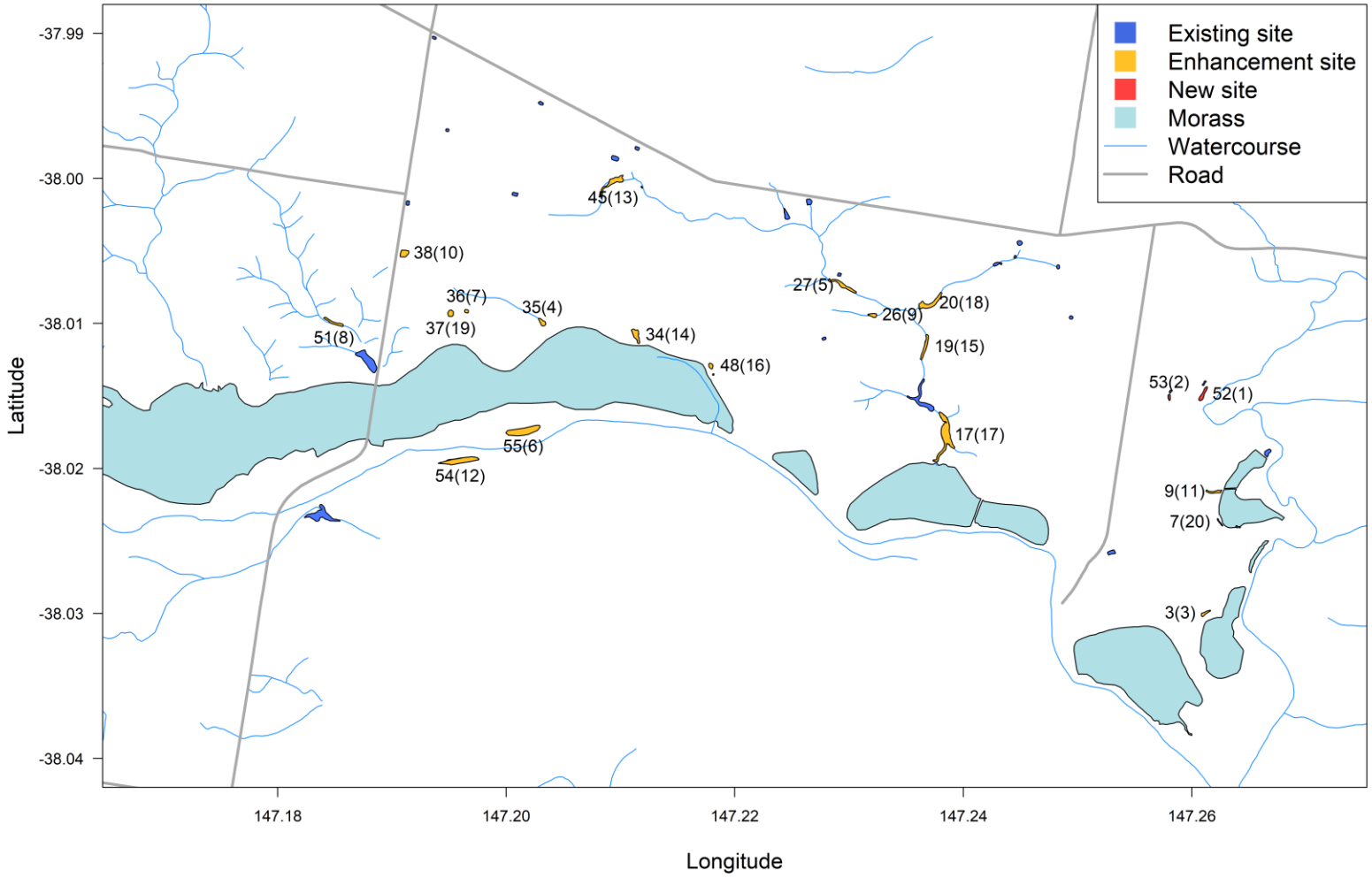


Figure 7. Ranking of potential management options for the Green and Golden Bell Frog (*Litoria aurea*) and Growling Grass Frog (*L. raniformis*) in the study area, based on the prioritisation analysis. Numbers outside of brackets are the site identifiers, as per Figure 6. Numbers in brackets are the prioritisation ranks for each site (from top = 1 to 20 = bottom).

In addition to the predicted benefit to the target species, a key consideration for prioritising which of the actions tested here to implemented is cost and feasibility (which were treated as equal in this analysis). The prioritisation completed for this project can be used to guide assessments of such trade-offs, with priority being judged against cost / feasibility in a qualitative ranking approach. However, the optimisation algorithm used for this project has the capacity to integrate cost explicitly, by setting a per-unit cost for each management action and assessing combinations of actions that fit within an overall budget (Scroggie *et al.* 2019). This represents a possible extension to this project and could be readily implemented in future.

Turning to the habitat management works themselves, considerable recent work has been completed on guidelines for habitat creation, enhancement or restoration for *L. aurea* and *L. raniformis*. For *L. aurea*, the work of Beranek *et al.* (2020) is the most recent and provides detailed guidelines for habitat construction and restoration activities that seek to mitigate the impacts of chytridiomycosis and exotic fish on this species. For *L. raniformis*, initial guidelines were provided by Heard *et al.* (2010), with updated and more detailed protocols for habitat management provided by DELWP (2017).

The prioritisation analysis completed here included specific enhancements considered feasible for these species at each site, and therefore, provide a blue-print for the specific actions to be undertaken at each site. However, one missing element is the provision of rock piles (more aptly, boulder piles) around wetlands as a means of mitigating chytrid impacts, passively managing riparian weeds and invasive emergent vegetation (particularly Typha *spp*. and *Phragmites australis*) and increasing microhabitat availability. Rock piles at the water's edge are important foraging and sheltering sites for both *L. aurea* (Garnham *et al.* 2015, Valdez *et al.* 2016, Valdez *et al.* 2017) and *L. raniformis* (Heard *et al.* 2008), and are thought to provide important basking areas for the thermoregulatory response of these frogs to chytrid fungus (allowing the frogs to increase their body temperature and thereby reduce or clear chytrid infections). For these reasons, rock piles have long been considered an important component of habitat creation and restoration activities for these frogs, and they continue to be (Darcovich and O'Meara 2008, DELWP 2017). Enhancing or providing rock piles was not explicitly considered in this project, as previous work has not enabled these fine-scale benefits to be estimated. However, I recommend experimenting with the provision of rock piles for *L. aurea* and *L. raniformis* in the study area for each of the reasons listed above.

Moreover, I encourage future habitat enhancement and creation works within the Avon-Perry River area to be treated as a management experiment. While the prioritisation that underpins this study is based on many years of research on the dynamics of *L. raniformis*, in particular, we know comparatively little about the response of this species to habitat management. Future works in the Avon-Perry River area could make a considerable contribution to gaining this understanding for *L. aurea* and *L. raniformis*.

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Appendix 1: Sites in the study area.

Sites include existing sites without enhancements considered, existing sites with possible enhancements and new sites. Current conditions are provided for existing sites, with values in brackets being the enhanced values for those sites at which they were considered feasible. Values provided for the two new sites are those considered feasible.

ID	Class	Enhance?	Easting	Northing	Type	Permanence (1-4)	Elevation (m)	Max depth (cm)	Emergent cover (%)	Submergent cover (%)	Floating cover (%)	Riparian cover (%)	Salinity (µS/cm)	Current source site?
1	Existing	No	522533	5790377	Morass	3	2	100	1	0	0	15	46400	No
2	Existing	No	523041	5790618	Morass	3	2	50	5	0	0	25	16000	No
3	Existing	Yes	522900	5790816	Dam	3 (2)	3	200 (50)	30 (0)	80 (0)	80 (0)	0 (0)	1840	No
4	Existing	No	523311	5791262	Morass	4	3	100	5	1	0	1	28537	No
5	Existing	No	523117	5791602	Morass	3	3	100	5	1	0	5	28000	No
6	Existing	No	523187	5791481	Dam	4	5	200	35	25	15	40	1591	Yes
7	Existing	Yes	523025	5791534	Pond	4 (4)	5	200 (100)	30 (60)	85 (85)	80 (0)	5 (5)	1636	No
8	Existing	No	523170	5791489	Pond	2	4	100	20	0	5	15	13170	Yes
9	Existing	Yes	523026	5791755	Dam	4 (3)	4	200 (100)	30 (0)	80 (0)	80 (0)	0 (0)	1970	No
10	Existing	No	523145	5791843	Morass	3	2	100	5	1	0	1	29394	No
11	Existing	No	523398	5792043	Dam	2	3	100	5	10	0	0	7770	No
12	Existing	No	522910	5792577	Pond	4	5	200	50	0	50	5	1150	Yes
13	Existing	No	522656	5792522	Pond	4	7	200	20	100	5	15	2102	No
14	Existing	No	522187	5791291	Dam	3	11	100	0	0	0	0	NA	No
15	Existing	No	521442	5791577	Morass	3	3	100	10	Dry	Dry	40	28000	No
16	Existing	No	520778	5791725	Morass	3	4	100	5	Dry	Dry	5	28000	No
17	Existing	Yes	520911	5792328	Dam	4 (4)	5	200 (100)	30 (5)	80 (0)	80 (0)	5 (5)	3280	No
18	Existing	No	520788	5792418	Dam	3	7	150	50	0	55	30	1686	No
19	Existing	Yes	520785	5792947	Marsh	4 (2)	9	200 (100)	30 (80)	80 (0)	80 (5)	20 (20)	4260	No
20	Existing	Yes	520765	5793184	Dam	4 (4)	13	150 (150)	30 (30)	80 (10)	80 (1)	10 (10)	8763	No
21	Existing	No	521312	5793499	Dam	3	16	100	45	0	0	5	4477	No
22	Existing	No	521463	5793552	Dam	2	17	50	30	0	0	1	416	No
23	Existing	No	521504	5793662	Dam	3	19	200	0	0	0	0	479	No

Appendix 1: Sites in the study area (continued).

ID	Class	Enhance?	Easting	Northing	Type	Permanence (1-4)	Elevation (m)	Max depth (cm)	Emergent cover (%)	Submergent cover (%)	Floating cover (%)	Riparian cover (%)	Salinity (µS/cm)	Current source site?
24	Existing	No	521795	5793479	Dam	3	24	100	0	0	0	0	NA	No
25	Existing	No	521896	5793091	Dam	2	23	100	0	0	0	0	NA	No
26	Existing	Yes	520383	5793112	Dam	4 (3)	13	200 (150)	30 (10)	80 (0)	80 (0)	0 (0)	231	No
27	Existing	Yes	520052	5793371	Dam	4 (3)	11	200 (100)	30 (10)	80 (0)	80 (0)	10 (10)	648	No
28	Existing	No	520117	5793425	Dam	3	11	200	10	0	0	0	198	No
29	Existing	No	519713	5793868	Dam	3	17	201-250	1	5	1	0	143	No
30	Existing	No	519881	5793981	Dam	3	18	201-250	0	0	0	0	87	No
31	Existing	No	519990	5792934	Dam	4	16	100	75	60	60	0	5640	No
32	Existing	No	519821	5791973	Morass	1	2	100	NA	NA	NA	5	28000	No
33	Existing	No	518566	5792611	Morass	3	2	150	30	0	0	10	10992	Yes
34	Existing	Yes	518554	5792972	Marsh	4 (3)	9	200 (50)	30 (70)	80 (0)	80 (0)	15 (15)	5045	No
35	Existing	Yes	517837	5793057	Dam	4 (3)	7	200 (200)	30 (5)	80 (0)	80 (1)	1 (1)	698	No
36	Existing	Yes	517247	5793149	Dam	4 (3)	26	200 (150)	30 (5)	80 (0)	80 (20)	0 (0)	901	No
37	Existing	Yes	517132	5793130	Dam	4 (3)	30	200 (150)	40 (40)	80 (20)	80 (30)	1 (1)	604	No
38	Existing	Yes	516773	5793594	Dam	4 (3)	35	200 (200)	30 (10)	80 (0)	80 (5)	1 (1)	645	No
39	Existing	No	516800	5793978	Dam	3	35	100	0	0	0	0	915	No
40	Existing	No	517624	5794046	Dam	3	30	100	0	0	0	0	NA	No
41	Existing	No	517104	5794540	Dam	3	38	100	0	0	0	0	NA	No
42	Existing	No	517005	5795236	Dam	3	39	100	0	0	0	0	NA	No
43	Existing	No	517820	5794742	Dam	3	38	100	0	0	0	0	NA	No
44	Existing	No	518389	5794317	Dam	3	29	200	1	0	0	0	362	No
45	Existing	Yes	518421	5794153	Dam	4 (3)	26	200 (100)	30 (15)	80 (0)	80 (5)	0 (0)	203	No
46	Existing	No	518600	5794099	Dam	3	26	100	15	0	5	0	218	No
47	Existing	No	518563	5794393	Dam	3	29	200	1	0	1	0	866	No
48	Existing	Yes	519129	5792716	Pond	4 (3)	8	200 (50)	30 (10)	80 (0)	80 (5)	0 (0)	19331	Yes
49	Existing	No	519144	5792662	Pond	3	5	100	20	0	0	0	29800	Yes
50	Existing	No	516473	5792815	Marsh	3	5	150	20	0	40	50	2740	Yes

Appendix 1: Sites in the study area (continued).

ID	Class	Enhance?	Easting	Northing	Type	Permanence (1-4)	Elevation (m)	Max depth (cm)	Emergent cover (%)	Submergent cover (%)	Floating cover (%)	Riparian cover (%)	Salinity (µS/cm)	Current source site?
51	Existing	Yes	516284	5793047	Dam	4 (3)	11	200 (150)	30 (30)	80 (0)	80 (1)	0 (0)	3570	No
52	New	NA	522912	5792507	Marsh	4	3	200	30	80	80	0	1150	No
53	New	NA	522649	5792481	Dam	4	7	200	30	80	80	0	2102	No
54	Existing	Yes	517209	5792006	Marsh	4 (2)	3	200 (100)	30 (15)	80 (0)	80 (0)	5 (5)	NA	No
55	Existing	Yes	517694	5792236	Marsh	4 (2)	3	200 (100)	30 (15)	80 (0)	80 (0)	10 (10)	NA	No
56	Existing	No	516132	5791592	Pond	4	6	200	5	0	30	25	9000	Yes

Appendix 2: Priority ranking of habitat management options.

Current conditions are provided for existing sites, with values in brackets being the enhanced values for those sites at which they were considered feasible. Values provided for the two new sites are those considered feasible.

ID	Class	Type	Permanence (1-4)	Elevation (m)	Max depth (cm)	Emergent cover (%)	Submergent cover (%)	Floating cover (%)	Riparian cover (%)	Salinity (µS/cm)	Selection frequency	Ranking
3	Existing	Dam	3 (2)	3	200 (50)	30 (0)	80 (0)	80 (0)	0 (0)	1840	0.86	3
7	Existing	Pond	4 (4)	5	200 (100)	30 (60)	85 (85)	80 (0)	5 (5)	1636	0.26	20
9	Existing	Dam	4 (3)	4	200 (100)	30 (0)	80 (0)	80 (0)	0 (0)	1970	0.59	11
17	Existing	Dam	4 (4)	5	200 (100)	30 (5)	80 (0)	80 (0)	5 (5)	3280	0.39	17
19	Existing	Marsh	4 (2)	9	200 (100)	30 (80)	80 (0)	80 (5)	20 (20)	4260	0.48	15
20	Existing	Dam	4 (4)	13	150 (150)	30 (30)	80 (10)	80 (1)	10 (10)	8763	0.31	18
26	Existing	Dam	4 (3)	13	200 (150)	30 (10)	80 (0)	80 (0)	0 (0)	231	0.63	9
27	Existing	Dam	4 (3)	11	200 (100)	30 (10)	80 (0)	80 (0)	10 (10)	648	0.73	5
34	Existing	Marsh	4 (3)	9	200 (50)	30 (70)	80 (0)	80 (0)	15 (15)	5045	0.53	14
35	Existing	Dam	4 (3)	7	200 (200)	30 (5)	80 (0)	80 (1)	1 (1)	698	0.81	4
36	Existing	Dam	4 (3)	26	200 (150)	30 (5)	80 (0)	80 (20)	0 (0)	901	0.67	7
37	Existing	Dam	4 (3)	30	200 (150)	40 (40)	80 (20)	80 (30)	1 (1)	604	0.3	19
38	Existing	Dam	4 (3)	35	200 (200)	30 (10)	80 (0)	80 (5)	1 (1)	645	0.6	10
45	Existing	Dam	4 (3)	26	200 (100)	30 (15)	80 (0)	80 (5)	0 (0)	203	0.56	13
48	Existing	Pond	4 (3)	8	200 (50)	30 (10)	80 (0)	80 (5)	0 (0)	19331	0.4	16
51	Existing	Dam	4 (3)	11	200 (150)	30 (30)	80 (0)	80 (1)	0 (0)	3570	0.64	8
52	New	Marsh	4	3	200	30	80	80	0	1150	1	1
53	New	Dam	4	7	200	30	80	80	0	2102	0.99	2
54	Existing	Marsh	4 (2)	3	200 (100)	30 (15)	80 (0)	80 (0)	5 (5)	NA	0.57	12
55	Existing	Marsh	4 (2)	3	200 (100)	30 (15)	80 (0)	80 (0)	10 (10)	NA	0.68	6