Abstract: Identification of habitat features that are strongly associated with the occurrence of threatened species is important in terms of predicting impacts of habitat change and identifying key habitats for conservation. In this paper, we apply habitat-based statistical models to predict occupancy patterns of the endangered Southern Bell Frog (Litoria raniformis) across inland New South Wales (Australia). Litoria raniformis previously occupied a wide range of natural and man-made waterbodies across a large geographic range, including floodplain wetlands, oxbow lagoons, irrigation canals and rice bays. Alteration of natural flooding regimes and livestock grazing have affected a large proportion of habitats within the historical range of L. raniformis, but it is not clear how these changes have influenced habitat occupancy patterns. Fifty-two waterbodies were surveyed for presence/absence of L. raniformis in 2001 and 2004. Step-wise logistic regression models were generated to select a subset of variables that could best predict occupancy. The interaction between wetland hydrology and complexity of aquatic vegetation, along with the complexity of fringing vegetation and water temperature were able to delineate between vacant and occupied waterbodies with an accuracy of 90% for vacant habitats and 70% occupied habitats. While this study demonstrated that a range of water body types are occupied by L. raniformis, these habitats do share common hydrological conditions and vegetation characteristics. Altered flooding regimes and reductions in the complexity of aquatic and fringing vegetation are likely to increase the probabilities of localised extinction events of L. raniformis. populations.

Habitat characteristics predict occupancy patterns of the endangered amphibian *Litoria raniformis* in flow regulated floodplain wetlands

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Word Count: 8530 Abstract

Identification of habitat features that are strongly associated with the occurrence of threatened species is important in terms of predicting impacts of habitat change and identifying key habitats for conservation. In this paper, we apply habitat-based statistical models to predict occupancy patterns of the endangered Southern Bell Frog (Litoria raniformis) across inland New South Wales (Australia). Litoria raniformis previously occupied a wide range of natural and man-made waterbodies across a large geographic range, including floodplain wetlands, oxbow lagoons, irrigation canals and rice bays. Alteration of natural flooding regimes and livestock grazing have affected a large proportion of habitats within the historical range of L. raniformis, but it is not clear how these changes have influenced habitat occupancy patterns. Fifty-two waterbodies were surveyed for presence/absence of L. raniformis in 2001 and 2004. Step-wise logistic regression models were generated to select a subset of variables that could best predict occupancy. The interaction between wetland hydrology and complexity of aquatic vegetation, along with the complexity of fringing vegetation and water temperature were able to delineate between vacant and occupied waterbodies with an accuracy of 90% for vacant habitats and 70% occupied habitats. While this study demonstrated that a range of water body types are occupied by L. raniformis, these habitats do share common hydrological conditions and vegetation characteristics. Altered flooding regimes and reductions in the complexity of aquatic and fringing vegetation are likely to increase the probabilities of localised extinction events of L. raniformis.

Key words: amphibian decline, habitat selection, logistic regression, *Litoria raniformis,* flow regulation

Introduction

Amongst the vertebrates, amphibians are notable for their high levels of habitat specialisation and sensitivity to environmental change (Vos and Stumpel 1996; Vos and Chardon 1998; Semlitsch 2000; Skelly *et al.* 2003). For many species, habitat occupancy has been linked to multiple habitat features at a range of spatial and temporal scales (Adams 1999; Anderson *et al.* 1999; Mazerolle and Villard 1999; Marsh *et al.* 2000; Trenham *et al.* 2001). At the wetland-scale, the cover and complexity of aquatic and fringing vegetation, wetland hydrology, water quality and the presence of predators can all influence species occupancy patterns (Healey *et al.* 1997; Adams 1999; Parris and McCarthy 1999b; Hazell *et al.* 2001; Jansen and Healey 2003). In addition to these wetland-scale habitat features, occupancy at patch-scale can be driven by proximity to habitats used for over-wintering or drought refuge and the spatial configuration of wetlands (Joly *et al.* 2001; Marsh and Trenham 2001; Skelly 2001; Guerry and Hunter 2002; Ficetola and De Bernardi 2004).

The often complex, scale dependant dynamics of wetland ecosystems and wetland dependant fauna present challenges for identifying the determinants of habitat occupancy by amphibians, and can confound prediction of the response of these animals to habitat alteration. In some instances it can be difficult to delineate between patterns of habitat use based on short-term movements to access local resources and occupancy of an area by a discrete population or subpopulation. In their review of amphibian metapopulations (Smith and Green 2005) argue that the basic assumption that the observed distribution pattern is due to habitat occupancy by a discrete subpopulation rather than habitat use within a patchy population is rarely tested and in many cases dispersal capabilities are underestimated. The failure to clearly differentiate between habitat use and occupancy is particularly problematic when identifying habitat predictors because the relative importance of the spatial configuration of wetlands can be overestimated, particularly for studies conducted at comparatively small spatial scales (Perret *et al.* 2003; Smith and Green 2006).

Habitat-based statistical models are the most commonly used methods of quantifying the relationship between habitat characteristics and the probability that a particular species will be present (Block *et al.* 1998; Guerry and Hunter 2002; Petit *et al.* 2003; Lecis and Norris 2004; Reich *et al.* 2004). Of the available statistical techniques, logistic regression is one of the most useful because it allows for inclusion of both continuous and categorical habitat data collected at a range of spatial scales and can be used to construct models which include more than one variable

in order to improve predictive power. Logistic regression is commonly used to model the relationships between amphibian occupancy and fine scale habitat features such as vegetation cover and water quality (Diller and Wallace 1999; Jansen and Healey 2003; Lecis and Norris 2004), as well as larger scale processes such as landscape composition (Hazell et al. 2001; Guerry and Hunter 2002; Porej, 2004).

The Southern Bell Frog (*Litoria raniformis*) was once common and widespread throughout south-eastern Australia. It occupied a range of natural and constructed wetland systems, throughout the coastal plains, cold tablelands regions, and inland floodplain systems of the Murray–Darling Basin (Mahony 1999; Pyke 2002). Over the past 30 years this species has undergone rapid declines and its formerly large geographic range has been reduced by more than half (Mahony 1999). *Litoria raniformis* is now listed as endangered under the New South Wales Threatened Species Conservation Act and Commonwealth Environment Protection and Biodiversity Conservation Act and the International Union for Conservation of Nature (IUCN).

Despite its decline, the range of habitat types occupied by *L. raniformis* remains diverse. Extant populations in cooler wetter areas are often associated with small permanent waterbodies including disused quarry pits and creeks that contain emergent vegetation (Heard *et al.* 2006). Populations occurring in relatively drier inland areas utilise large floodplain wetland systems and irrigation infrastructure, particularly rice bays and canals. These inland systems are characterised by broad-scale seasonal inundation, extreme daily temperature fluctuations and periods of drought (Wassens *et al.* 2007).

The key mechanisms responsible for declines of *L. raniformis* also vary across its range. A fungal pathogen (*Batrachochytrium dendrobatidis*) is likely to have contributed to declines in the cold tablelands regions (Osborne *et al.* 1996), but not in inland areas where high summer temperatures are likely to limit its occurrence (Kriger *et al.* 2007). Two species of exotic fish, the Mosquito Fish (*Gambusia holbrooki*) and the Common Carp (*Cyprinus carpio*) are widespread throughout south-eastern Australia. Mosquito Fish are known to eat small tadpoles of a range of frog species and have been shown to affect survivorship in tank experiments (Pyke and White 2000; Hamer *et al.* 2002b). Field studies however, suggest that the presence of Mosquito Fish does not appear to limit the occupancy of the closely related species *Litoria aurea* (Hamer *et al.* 2002a). Although there have been no studies on the direct impacts of the Common Carp on tadpole survival, they are known to reduce water quality and damage aquatic vegetation (Roberts *et al.* 1995; King *et al.* 1997), both of which could impact recruitment success (Beebee 1981; Hazell *et al.* 2001; Gillespie 2002).

In addition to the threats posed by *B. dendrobatidis* and introduced fish, river regulation has greatly altered the hydrological characteristics of many wetland systems, particularly floodplain wetlands and ox-bow lagoons, that historically supported *L. raniformis*. Hydrological changes resulting from flow regulation include reduced frequency of inundation, reduced connectivity between wetlands, and in some instances increased water permanence. For example, flooding frequency across the mid-Murrumbidgee floodplain has been reduced from a periodicity of 1.5 years to 2.2 years since 1980 (Page *et al.* 2005). There has also been a decrease in the frequency of very large floods that would normally connect wetlands across the floodplain, which has led to isolation of wetlands higher on the floodplain (Arthington and Bradley 2003). Whilst some former habitats are now drier for longer periods, high summer water levels in many regulated river systems have resulted in the conversion of seasonally flooded wetlands to permanent waterbodies (Kingsford *et al.* 2004). Altered flooding regimes have contributed to declines of wetland-dependent species, such as waterbirds (Kingsford 2000), lowland fish (Gehrke and Harris 2001) and macroinvertebrates (Quinn *et al.* 2000). Flow regulation is also likely to have contributed to local extinctions of *L. raniformis* in inland areas (Wassens 2008), but the extent to which wetland hydrology presently drives occupancy patterns is unknown.

The extent of habitat modification and limited knowledge of the present distribution of *L. raniformis* populations within its historic range make it difficult to determine which wetlands are likely to support populations. This limits our ability to target wetlands for environmental watering or to predict the outcomes of continued hydrological modification. The aim of this study is to describe wetland habitats important to *L. raniformis* in semi-arid zones and to identify specific habitat features that could be used to predict occupancy across multiple wetland types.

Methods

Study area

The study area encompasses wetland and irrigation systems in the middle and lower reaches of the Murrumbidgee River floodplain and its distributaries, within the Murray-Darling Basin of south-eastern Australia (Figure 1). The climate of the area is classed as semi-arid with hot dry summers (mean maximum 32.2°C) and cool winters (mean maximum 14.2°C). Annual median rainfall ranges from 429 mm at Narrandera in the on the eastern edge of the study area, to 315 mm at Balranald in the west. Rainfall is evenly distributed throughout the year, but evaporation rates far exceed precipitation during the summer months. Rainfall is highly variable across years and with drought conditions are common.

The mid and lower Murrumbidgee floodplain is a flat, alluvial plain (Page *et al.* 1996). Away from major rivers, creek lines and wetlands systems vegetation is dominated by grasslands and chenopod shrub. The Murrumbidgee River derives most of its water from snow melts and rainfall in the upper catchment which means that major flooding is independent of local rainfall. The Murrumbidgee River is regulated by Blowering and Burrinjuck Dams in the upper catchment, which controls the release of water for irrigation and environmental purpose (Page *et al.* 1996). Wetlands within the semi-arid are typically large terminal wetlands at the end of creek systems or filled via a lateral connection to the river and its distributaries. Rain-fed ponds can occur at any time of the year following heavy rains and generally have short hydroperiods (less than 4 weeks) due to the high evaporation rates.

The study area incorporates four key regions; the Murrumbidgee Irrigation Area (MIA), Coleambally Irrigation Area (CIA), Mid-Murrumbidgee wetlands and Lowbidgee floodplain. The Murrumbidgee Irrigation Area lies to the north of the Murrumbidgee River and covers an area of over 200,000 Ha. The MIA contains a number of RAMSAR listed, Black Box (*Eucalyptus largiflorens*) and open grassy wetlands including Fivebough and Tuckerbil Swamps and the nationally important Barron Box Swamp, as well as extensive areas of flood irrigated cereal, particularly rice and orchards. The Coleambally Irrigation District (CIA) lies to the south of the Murrumbidgee River covering an area of 80,000 Ha; the CIA has been extensively cleared of its native Black Box and Lignum (*Muelenbeckia florulenta*) wetlands and is dominated by flood irrigated rice. The Mid-Murrumbidgee wetlands are a series of ox-bow lagoons, surrounded by River Red Gum (*Eucalyptus camaldulensis*) forest, which are connected to the Murrumbidgee River during high flows (Kingsford *et al.* 2003). The Lowbidgee floodplain is a large inland delta system at the end of the Murrumbidgee River which acts as a water retention basin, reducing peak flows downstream. This delta system forms the nationally significant Lowbidgee Wetland system which incorporates over 200, 000 Ha of flooded River Red Gum forest, Open spike rush (*Eleocharis sphacelata*) wetlands, Black Box/Lignum and Lignum wetlands (Kingsford and Thomas 2001).

Waterbodies within all of the regions assessed in this study have been modified to some extent through the regulation of river flows, the construction of irrigation canals and regulator structures, or conversion to water storages. Within the two irrigation areas many of the larger seasonally flooded wetland systems such as Barren Box Swamp have been converted to permanent water storages, while irrigation canals and flooded rice bays have increased the availably of standing water over large areas (Kingsford 2000). Wetland systems in the Mid-Murrumbidgee wetlands are all highly modified due to the regulation of river flows and the decreased frequency of overbank flood events (Briggs *et al.* 1997; Jansen and Healey 2003). Wetland systems in the lower reaches of the Murrumbidgee have also been modified by the development of flood cropping systems and the redistribution of flood water across the floodplain (Kingsford 2000; Kingsford and Thomas 2001).

Site selection

A total of 52 waterbodies were surveyed (see Figure 1). We attempted to sample the all major wetlands listed under the Directory of Nationally Important Wetlands that occurred within the study region and contained water in October 2001. These included Fivebough and Tuckerbil wetlands, the mid-Murrumbidgee wetlands and the Lowbidgee wetlands.

In addition to Fivebough and Tuckerbil Swamps which are open grassy wetland systems, we surveyed all major flooded Black Box wetlands in the CIA and MIA (n=7), and all major water storages (Barren Box Swamp and Lake Wyngan) (n=2). In addition to these large wetlands, smaller dams (<5Ha) were selected on a stratified random basis from with all study regions (n=5). Because *L. raniformis* is known to utilise irrigation infrastructure (Pyke 2002; Wassens *et al.* 2007), we also selected rice bays complexes (rice bays and on-farm canals) (n=17) and major irrigation canals (n=4) from within the CIA and MIA. These irrigation sites were largely selected using a stratified random approach but we were also limited to sites where landholders were prepared to grant access. All of the ox-bow lagoons containing water within the Mid Murrumbidgee wetlands were surveyed (n=6). The Lowbidgee floodplain covers and area of approximately 200,000Ha. In this region we used a stratified-random approach to select wetlands from each vegetation type, these included, Lignum wetlands (n=3), Black Box/Lignum wetlands (n=3), River Red Gum/Spike Rush wetlands (n=4) and ox-bow lagoons (n=1). Only one ox-bow lagoon was surveyed in the Lowbidgee floodplain because it was the only one containing water during this study.

Field surveys were undertaken during October 2001, January 2002, October 2003 and January 2004. Surveyed were conducted in October and January to coincide with the peak calling and activity periods of *L. raniformis* in semi-arid regions (Wassens *et al.* 2007). Weather conditions were similar during October 2001 and 2004 temperatures were mild, with a mean overnight minimum of 8.3C to a daily maximum of 23.8C. Temperatures during January 2001 and 2004 were warm to hot with a mean overnight minimum of 16.8C and mean daily maximum of 32.7C.

Surveys for *Litoria raniformis*

The wetland study sites targeted in this study ranged in size from 2ha to over 3000ha (mean for all study sites 178ha). To ensure that each study site was surveyed comprehensively, we used between 5 and 10, 50m transects placed at roughly equal distances around the edge of each water body. Surveys along each 50m transect were conducted after dark using a combination of visual-encounter and audio-survey techniques (Heyer et al. 1994). Each transect was surveyed by sweeping a 25 W spotlight from side to side along its length. The spotlight was also used to actively search for frogs in the water, along the water's edge, amongst vegetation, and under loose soil, timber and rocks. In addition, audio-surveys were conducted along each transect; these involved call play back for two minutes followed by five minutes listening for calls. Each study site was surveyed for a minimum of one hour for smaller wetlands to a maximum of four hours for larger wetlands on each of the four survey occasion.

Habitat measurements

Vegetation and water chemistry was assessed at each of the four survey times along the *L. raniformis* survey transects. At this time this study commenced the distribution and habitat requirements of *L. raniformis* outside the southern tablelands were poorly known. Wetland vegetation characteristics, such as percent cover of vegetation, diversity of microhabitats, water quality and hydrology have been shown to influence amphibian occupancy patterns (Boyer and Grue 1995; Gillespie 1996; Griffiths 1997; Healey *et al.* 1997; Babbitt and Tanner 1998; Parris and McCarthy 1999a) and Healy *et al.* (1997) in particular had demonstrated the importance of vegetation complexity in structuring amphibian communities within the Murrumbidgee floodplain. Given the size of our study area, we aimed to select variables that could be applied across the range of different wetland types and regions and were likely to be biological meaningful. Because vegetation communities differed greatly across the study area, measurements of that focused on specific species or even functional were not appropriate because they could not be applied across all wetland types. Instead we used standard measures of wetland functional composition, water quality and hydrology (Spencer *et al.* 1998). The characteristics of aquatic and fringing vegetation in terms of cover, complexity and height were measured. Fringing vegetation was defined as any vegetation within 2 m of the water body, while aquatic vegetation was any vegetation growing wholly within the water body. Percent cover for both aquatic and fringing vegetation was estimated one metre from the water line for ten 1 m^2 quadrats located approximately 5 m apart along the survey transects. The mean value of these replicates was recorded. The number of layers

of both aquatic and fringing vegetation was estimated in each of the 10 quadrats. Layers of aquatic vegetation was a count of the number of different vegetation growth forms according to (Sainty 2003); submerged vegetation, attached floating vegetation, free floating vegetation, short emergent vegetation (less than 50 cm tall) and tall emergent vegetation (greater than 50 cm), inundated shrubs (e.g. Lignum and Nitre Goosefoot) and inundated trees

(e.g. River Red Gum and Black Box). The complexity of fringing vegetation was a count of different vegetation layers; short grasses (less than 10 cm), tall grasses (greater than 10 cm), short forbs (less than 10 cm), tall forbs (greater than 10 cm), shrubs (Lignum and Nitre Goosefoot) and trees (River Red Gum and Black Box). Wetland area was taken from existing GIS data layers supplied by the Murrumbidgee Irrigation Cooperative and the Coleambally Irrigation Cooperative, the NSW atlas of significant wetlands, as well as reports (Briggs *et al.* 1997). ArcMap version 9.3 was used on all occasions. Water chemistry was measured on each sample occasion (n=4) at each of the survey transects between 6am and 11am using a Hydrolab water quality metre. Water temperature (°C), electrical conductivity ($mScm^{-1}$), turbidity (NTU), depth (cm) and pH were recorded. Dissolved oxygen was recorded but has not been included in the analysis, because the expected diurnal variation in dissolved oxygen levels invalidates site comparisons. Fish were not surveyed because the very intensive survey methods required to census fish in large wetlands was prohibitive for a study of this scale.

Because of the hot climatic conditions of the region, waterbodies typically undergo relatively high levels of seasonal or long-term fluctuation in depth and area. For the purposes of this study, three broad hydrological classes were defined. *Permanent waterbodies* (n = 17) contained water continuously for the previous five years. *Seasonally flooded wetlands* (n = 25) flooded to some extent every year but may dry for short periods (less than 3 months) between annual floods. *Ephemeral wetlands* (n = 10) flooded only during large over-bank flows or heavy rain and may not contain water every year.

Data analysis

The relationship between the presence of *L. raniformis* at each site and the measured environmental variables was modelled by fitting a regression model with a logistic function and binomial error function with LOGLIT link (S-Plus version 7). This approach models the relationship between a presence/absence dependent variable and continuous or categorical independent variables occurring across a range of spatial and temporal scales (Hosmer and Lemeshow 2000).

Model development

Habitat models were developed to discriminate between locations where *L. raniformis* were present and those where they were absent. Because the number of sample sites (n=52) was relatively small compared to the number of measured habitat variables (n=11) the initial sets of variables were culled using a two-step process according to (Hosmer and Lemeshow 2000). First, pooled variance two sample t-tests (S-Plus version 7) were used to test whether continuous habitat variables measured at the study sites where *L. raniformis* was present differed from those where it was absent. Habitat variables were excluded from further analysis if the t-test *p*-value was greater than 0.2 (Hosmer and Lemeshow 2000). This cut off point was selected because the use of the tradition cut off points of 0.05 at the early stages of model development can exclude variables that are biologically meaningful within a final model (Mickey and Greenland 1989).

As a second cull step, univariate logistic regression models (preliminary main effects model) were developed for each of the remaining variables (those with p-values <0.2). The fits of the univariate model were tested using Pearson's chi-square goodness-offit test and the significance level of the Log Likelihood ratio (S-Plus version 7). Variables that failed the goodness of fit test and had a significance level of less than 0.1 were excluded from subsequent multivariate modeling. This additional culling step was undertaken to reduce the likelihood of over-fitting variables to the model. Given that wetland hydrology can influence vegetation complexity (Casanova and Brock 2000), we also modelled the relationship between occupancy by *L. raniformis* and the interaction between wetland hydrology and the number of layers of aquatic vegetation.

A backwards stepwise logistic regression (S-Plus version 7) with a probability of variable removal of 0.1 was then developed to select the best subset of the remaining variables that best predicted the probability of occupancy of *L. raniformis*. The importance of each variable within the model was determined by assessing the change in the log-likelihood ratio when that variable was removed from the model. The Wald statistic was used in conjunction with the log-likelihood ratio to assess the significance of each variable within the model. Two tests were used to assess the fit of the model at each step, the Hosmer and Lemeshow goodness-of-fit statistics (Hosmer and Lemeshow 2000) and the Pearson Chi-square statistic. In addition, Akaike Information Criterion (AIC) was used to identify the most parsimonious model. AIC is calculated as: $AIC = k + n [Ln(2(pi) RSS/(n-k)) +1]$ .Where k is the number of model parameters and RSS is the Residual Sum of Squares and is used to select between multivariate models   where (k<1) (S-Plus version 7).

Results

Litoria raniformis were found at 21 of the 52 sites surveyed between October 2001 and January 2004. Occupied study sites included seasonally-flooded River Red Gum and Black Box/Lignum and Lignum wetlands in the Lowbidgee floodplain, and seasonally-flooded rice bays and irrigation canals in the Coleambally Irrigation Area. *Litoria raniformis* was absent from a number of waterbodies where it had been recorded between 1960 and 1980 including the Mid-Murrumbidgee wetlands and Barren Box Swamp in the Murrumbidgee Irrigation Area. The probability of detection was high, with the exception of two sites; *L. raniformis* was either detected on all four occasions or never detected. *Litoria raniformis* was detected on both survey occasions in 2001 at Suicide and Chainman's Swamps in the Lowbidgee floodplain, but was not detected in 2004. Both of these wetlands dried out after the January 2001 surveys and had been continuously dry for nearly 3 years by 2004 and were therefore excluded from the 2004 surveys.

Seven of the 11 measured habitat variables were included for further analysis on the basis of the two-tailed t-test results (Table 1). A univariate logistic regression model was constructed for each of the remaining seven continuous habitat variables (that had significance values of less than 0.2 from the two-tailed t-tests), the two categorical variables (wetland hydrology and habitat type), and the interaction between wetland hydrology and number of layers of aquatic vegetation were also included (see table 1). Overall, the number of aquatic layers was the most successful predictor of *L. raniformis* occupancy with an overall classification success of 75%. The probability of occupancy increased to over 0.6 once the number of layers of aquatic vegetation was three or more (Figure 2). However, this relationship was also influenced by wetland hydrology because seasonally flooded wetlands generally had a greater number of layers of aquatic vegetation than permanent or ephemeral wetlands. Thus the interaction between the categorical variable, wetland hydrology, and number of layers of aquatic vegetation was also significant with the probability of occupancy highest in seasonally flooded that also had more complex vegetation (Figure 2). The probability of occupancy also increased with increasing number of layers of fringing vegetation and sites were less likely to be occupied if they contained less than two layers. Vegetation height was also significant within the preliminary main effects model, but the spread of the values was limited, resulting in relatively poor predictive power once vegetation height increased to over 40 cm. Of the measured water quality variables the probability of occupancy increased with increasing water temperature, but this relationship was comparatively weak because there were only a small number of sites with low water temperatures (less than 20°C). Turbidity was also related to the probability of occupancy, with the probability of occupancy decreasing with increasing turbidity. The probability of occupancy decreased with increasing pH but while this variable was significant it was excluded from further analysis because it failed the Chi-Square and Hosmer and Lemeshow test (= 20.221, p < 0.05).

Conductivity was not significantly related to the probability of   occupancy.

Variable selection

The purpose of building multivariable models is to select the smallest subset of variables that best explain the data (Hosmer and Lemeshow 2000). To achieve this goal, all the significant variables and their interactions from the univariate logistic regression models were included in a backward stepwise regression. On the basis of the results of the backwards stepwise regression (Table 2), the following habitat variables were significant in explaining presence/absence of *L. raniformis*: the interaction between hydrology and number of layers of aquatic vegetation (HYDRO by

LAY_AQU), the number of layers of fringing vegetation (LAY_FRI) and water temperature (TEMP). This combination of variables correctly classified 70% of sites where *L. raniformis* were present and had the lowest AIC value. The fit of the model at step 4 can be considered satisfactory because the Nagelkerke R-Square was high ($R^2 = 0.637$) and the Hosmer and Lemeshaw test was not significant. The removal of fringing vegetation from the model at step 5 lead to increases in the AIC value and resulted in a poorly fitting model.

Discussion

Occupancy of waterbodies by *Litoria raniformis* was strongly linked to seasonal flooding regimes and vegetation complexity. The interaction between these two variables was a good predictor of the probability of occupancy by *L. raniformis* and this relationship held regardless of whether the waterbodies were man-made, e.g. rice bays complexes or canals, or naturally occurring. The interaction between wetland hydrology and vegetation complexity is expected because hydrology plays a major role in structuring aquatic vegetation (Casanova and Brock 2000; Warwick and Brock 2003). In general seasonally flooded waterbodies have lower predator densities (Adams 2000) and greater vegetation complexity when compared with permanent wetlands (Casanova and Brock 2000; Warwick and Brock 2003) which may increase their value for amphibians. However, permanent waterbodies were still occupied if they contained more complex aquatic vegetation which suggests that vegetation complexity may reduce the impact of higher predator densities. Both permanent and seasonally flooded wetlands were more likely to be occupied by *L. raniformis* than ephemeral waterbodies. *Litoria raniformis* has limited capacity to survive through extended dry periods (Pyke 2002), which is reflected in its absence from sites that have low flooding frequencies.

 The complexity of fringing vegetation was also important in predicting occupancy by *L. raniformis*. Individuals utilise fringing vegetation as both daytime shelter sites and over-winter sites (Wassens *et al.* 2008). Sites with a greater number of layers of fringing vegetation provide better quality shelter with more constant temperature and greater protection from the elements (Buttemer *et al.* 1996). Heavy grazing by livestock can remove fringing vegetation (Jansen and Robertson 2001), which may contribute to declines of *L. raniformis* in some areas. However, the impact of livestock on fringing vegetation cover varies between wetlands due to differences in the palatability of fringing vegetation, for example a cattle grazing has little impact on the complexity and cover in Lignum wetlands because this vegetation is not very palatable. In addition, livestock grazing was not the only mechanism for removing fringing vegetation; slashing, spraying and burning are commonly used to reduce vegetation height around irrigation canals and rice bays. Because the mechanisms for reducing vegetation cover varied across the study area, the use of metrics such as vegetation height and complexity are more useful then identification of specific activities such as grazing when modelling occupancy patterns of *L. raniformis*.

The complexity of aquatic and fringing vegetation were better predictors of occupancy by *L. raniformis* than the percent cover. Other studies have used the abundance of particular types of vegetation to successfully predict occupancy by the closely related species, *Litoria aurea* and there is little doubt that vegetation can be important in maintaining amphibian populations (Hamer *et al.* 2002a; Jansen and Healey 2003). However, despite the differences in vegetation communities assessed in this study, the percent cover of fringing and aquatic vegetation did not differ greatly between study sites. This lack of variability in percent cover between wetlands means that it is not a useful predictor of occupancy by *L. raniformi*s in semi-arid regions.

Of the measured physicochemical parameters, *L. raniformis* was more likely to occupy wetlands with warmer water and lower turbidity. This differs from studies of the closely related *L. aurea* for which physicochemical factors did not influence occupancy (Hamer *et al.* 2002a). Temperature has little impact on the activity patterns of *L. raniformis* in semi-arid areas (Wassens *et al.* 2008) and the temperature ranges experienced in this study were all well within the normal tolerance limits for this species (Pyke 2002). A significant relationship between occupancy and water temperature is most likely to occur because *L. raniformis* favours large, shallow waterbodies which tend to have higher temperatures than deep, permanent waterbodies. As a result the use of water temperature alone to predict occupancy needs to be treated with caution. However, including water temperature within the final multivariate model greatly increases predictive power, probably because water temperature is a good descriptor of a range of other wetlands attributes. The probability of occupancy by *L. raniformis* was significantly correlated with turbidity when it was modelled as a single variable in the preliminary main effects model. However turbidity was not included in the final multivariate model because it is strongly correlated with water temperature.

Spatial autocorrelation between nearby sites can be important when modelling occupancy patterns, particularly when modelling occupancy patterns within a metapopulation or patchy population because occupancy at one water body can be influenced by local movements between waterbodies (Hanski 2001; Trenham *et al.* 2001; Ficetola and De Bernardi 2004; Smith and Green 2005). For example, Hamer *et al*. (2002) found that waterbodies were more likely to be occupied by *L. aurea* if they were within 50m of the next occupied water body. However, the spatial scale at which a single "habitat patch" is defined is critical when determining the importance of the distance between patches in predicting occupancy (Smith and Green 2005). This study treated large, complex wetland systems as a single patch, the presence of *L. raniformis*, habitat and water chemistry variables data was collected from multiple transects over four time periods and were than averaged to give a single value for each wetland. To put this into a spatial context, the entire study area assessed by Hamer *et al*. (2002) was smaller than the largest "habitat patch" assessed in the current study. The rational for this approach is well supported by studies of *L. raniformis* in semiarid areas which demonstrate that, in the absence of a major flood event, significant temporal changes in the spatial distribution of *L. raniformis* occur within but not between large wetland complexes (Wassens *et al.* 2007; Wassens *et al.* 2008). Movement rates between waterbodies in semi-arid areas are typically very low, because of the large distances, high evaporation rates and extreme temperatures. However, large flood events connect wetlands over large areas, often forming a single continuous water body which can be several thousand hectares in area, while these events occur infrequently they are likely to be a key mechanism for driving amphibian dispersal and recolonisation patterns between wetland systems (Wassens *et al.* 2008). In these instances methods that quantify the frequency of connectivity between wetlands may be a more useful measure of the probability of occupancy than spatial measures alone. The capture of LIDAR data throughout the study area will ultimately make it possible to model the annual distribution of floodwaters across the study region. Assessment of the links between *L. raniformis* occupancy and connectivity via flood waters will make a valuable contribution to our understanding of population processes in semi-arid areas and should be considered in future analysis when these data are available.

The differences in detection probability between this study and that by (Heard *et al.* 2006) are also a function of the differing spatial scales at which the two studies were conducted. Heard *et al.* (2006) assessed the probability of encountering individuals along individual 25m transects, which were treated as independent even though the majority were located along a single continuous creek line. This study assessed occupancy patterns at 52 waterbodies (mean area 178ha), using multiple 50m transects. Transects within a single wetland study site were not considered to be independent and the outcomes of surveys along each transect were grouped to give a single value for each study site. This strategy was used because it reduced interference from short-term changes in the distribution of individuals within the water body.

This study aimed to describe wetland habitats important to *L. raniformis* in semi-arid zones and to identify specific habitat features that could be used to predict occupancy across multiple wetland types. A model incorporating wetland hydrology, vegetation complexity and water temperature successfully predicted occupancy patterns across the diverse range of wetland types included in this study. The study demonstrates that despite occupying a wide geographic range and multiple wetland types *L. raniformis* has comparably specialised requirements in terms of hydrological conditions and vegetative. Alteration of these conditions as a result of river regulation and water diversions may have contributed to the loss of *L. raniformis* populations in some areas, for example the loss of *L. raniformis* from Barren Box Swamp coincided with its conversion from a seasonally flooded wetland to permanent water storage in the 1970's (Wassens 2008). The majority of wetlands presently occupied by *L.*

raniformis are under threat due to continuing reductions in the frequency and extent of flood events as a result of to flow regulation and water diversions (Kingsford 2000; Kingsford and Thomas 2001). In many regions, the flooding requirements of extant

L. raniformis populations are not explicitly considered when planning environmental water releases. The lack of a long-term wetland management plan that addresses the conservation of *L. raniformis* populations in the key floodplain habitats means that extant populations are at constant risk of local extinction due to a lack of wetland flooding.

References

Adams M. J. (1999) Correlated factors in amphibian decline: exotic species and habitat change in western Washington. *Journal of Wildlife Management* **63**, 1162-71.

Adams M. J. (2000) Pond permanence and the effects of exotic vertebrates on anurans. *Ecological Applications* **10**, 559-68.

Anderson A. M., Haukos D. A. & Anderson J. T. (1999) Habitat use by anurans emerging and breeding in playa wetlands. *Wildlife Society Bulletin* **27**, 759-69.

Arthington A. H. & Bradley J. P. (2003) Flow restoration and protection in Australian rivers. *River Research and Applications* **19**, 377-95.

Babbitt K. J. & Tanner G. W. (1998) Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. *Oecologia* **114**, 258-62.

Beebee T. J. C. (1981) Habitats of the British amphibians (4): Agricultural lowlands and a general discussion of requirements. *Biological Conservation* **21**, 127-39.

Block W. M., Morrison M. L. & Scott P. E. (1998) Development and evaluation of habitat models for herpetofauna and small mammals. *Forest Science* **44**, 430-7.

Boyer R. & Grue C. E. (1995) The need for water quality criteria for frogs. *Environmental Health Perspectives* **103**, 352-7.

Briggs S. V., Thorton S. A. & Lawler W. G. (1997) Relationships between hydrological control of River Red Gum wetlands and waterbird breeding. *Emu* **97**, 31
42.

Buttemer W. A., van der Wielen M., Dain S. & Christy M. (1996) Cutaneous properties of the Green and Golden Bell Frog *Litoria aurea*. *Australian Zoologist* **30**, 134-8.

Casanova M. T. & Brock M. A. (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology* **147**, 237-50.

Ficetola G. F. & De Bernardi F. (2004) Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation* **119**, 219-30.

Gehrke P. C. & Harris J. H. (2001) Regional-Scale Effects of Flow Regulation on Lowland Riverine Fish Communities in New South Wales, Australia. *Regulated Rivers-Research & Management* **17**, 369-91.

Gillespie G. R. (1996) Distribution, habitat and conservation status of the Green and Golden Bell Frog *Litoria aurea* (Lesson 1829) (Anura: Hylidae) in Victoria. *Australian Zoologist* **30**, 199-207.

Gillespie G. R. (2002) Impacts of sediment loads, tadpole density, and food type on the growth and development of tadpoles of the Spotted Tree Frog *Litoria spenceri*: an in-stream experiment. *Biological Conservation* **106**, 141-50.

Griffiths R. A. (1997) Temporary ponds as amphibian breeding habitats. *Marine and freshwater ecosystems* **7**, 119-26.

Guerry A. D. & Hunter M. L. (2002) Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* **16**, 745-54.

Hamer A. J., Lane S. J. & Mahony M. J. (2002a) Management of freshwater wetlands for the endangered Green and Golden Bell Frog (*Litoria aurea*): roles of habitat determinants and space. *Biological Conservation* **106**, 413-24.

Hamer A. J., Lane S. J. & Mahony M. J. (2002b) The role of introduced Mosquitofish (*Gambusia Holbrooki*) in excluding the native Green and Golden Bell Frog (*Litoria aurea*) from original habitats in south-eastern Australia. *Oecologia* **132**, 445-52.

Hanski I. (2001) Population dynamic consequences of dispersal in local populations and metapopulations. In: *Dispersal* (eds J. Clobert, E. Danchin, A. A. Dhondt and J.
D. Nichols) pp. 283-98. Oxford University Press, Oxford.

Hazell D., Cunnningham R., Lindenmayer D., Mackey B. & Osborne W. (2001) Use of farm dams as frog habitat in an Australian agricultural landscape: factors affecting species richness and distribution. *Biological Conservation* **102**, 155-69.

Healey M., Thompson D. & Robertson A. (1997) Amphibian communities associated with billabong habitats on the Murrumbidgee floodplain, Australia. *Australian Journal of Ecology* **22**, 270-8.

Heard G. W., Robertson P. & Scroggie M. P. (2006) Assessing detection probabilities for the endangered growling grass frog (*Litoria raniformis*) in southern Victoria. *Wildlife Research* **33**, 557–64

Hosmer D. W. & Lemeshow S. (2000) *Applied logistic regression*. John Wiley & Sons, New York.

Jansen A. & Healey M. (2003) Frog communities and wetland condition: relationships with grazing by domestic livestock along an Australian floodplain river. *Biological Conservation* **109**, 207-19.

Jansen A. & Robertson A. I. (2001) Relationships between livestock management and the ecological condition riparian habitats along an Australian floodplain river. *Journal of Applied Ecology* **38**, 63-75.

Joly P., Miaud C., Lehmann A. & Grolet O. (2001) Habitat matrix effects on pond occupancy in newts. *Conservation Biology* **15**, 239-48.

King A. J., Robertson A. I. & Healey M. R. (1997) Experimental manipulations of the biomass of introduced carp (*Cyprinus carpio*) in billabongs .1. Impacts on water-column properties. *Marine and Freshwater Research* **48**, 435-43.

Kingsford R. T. (2000) Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecology* **25**, 109-27.

Kingsford R. T., Brandis K., Thomas R., Crighton P., Knowles E. & Gale E. (2003) The Distribution of Wetlands in New South Wales. Queanbeyan.

Kingsford R. T., Jenkins K. M. & Porter J. L. (2004) Imposed hydrological stability on lakes in arid Australia and effects on waterbirds. *Ecology* **85**, 2478-92.

Kingsford R. T. & Thomas R. F. (2001) *Changing water regimes and wetland habitat on the Lower Murrumbidgee floodplain of the Murrumbidgee River in Arid Australia*. NSW National Parks and Wildlife Service, Sydney.

Kriger K. M., Pereoglou F. & Hero J. (2007) Latitudinal variation in the prevalence and intensity of Chytrid (*Batrachochytrium dendrobatidis*) infection in Eastern Australia. *Conservation Biology* **21**, 1280-90.

Lecis R. & Norris K. (2004) Habitat correlates of distribution and local population decline of the endemic Sardinian newt *Euproctus platycephalus*. *Biological Conservation* **115**, 303-17.

Mahony M. J. (1999) Review of the declines and disappearances within the Bell Frog species group (*Litoria aurea* species group) in Australia. In: *Declines and disappearances of Australian frogs* (ed A. Campbell) pp. 81-93. Environment Australia, Canberra.

Marsh D. M., Rand A. S. & Ryan M. J. (2000) Effects of inter-pond distance on the breeding ecology of tungara frogs. *Oecologia* **122**, 505-13.

Marsh D. M. & Trenham P. C. (2001) Metapopulation dynamics and amphibian conservation. *Conservation Biology* **15**, 40-9.

Mazerolle M. J. & Villard M. A. (1999) Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience* **6**, 117-24.

Mickey J. & Greenland S. (1989) A study of the impact of confounder-selection criteria on effect estimation. *American Journal of Epidemiology* **129**, 125-37.

Osborne W. S., Littlejohn M. J. & Thompson S. A. (1996) Former distribution and apparent disappearance of the *Litoria aurea* complex from the Southern Tablelands of New South Wales and the Australian Capital Territory. *Australian Zoologist* **30**, 190 8.

Page K., Read A., Frazier P. & Mount N. (2005) The effect of altered flow regime on the frequency and duration of bankfull discharge: Murrumbidgee River, Australia. *River research and applications* **21**, 567-78.

Page K. J., Nanson G. C. & Price D. M. (1996) Chronology of Murrumbidgee River palaeochannels on the Riverine Plain, southeastern Australia. *Journal of Quaternary Science* **11**, 311-26.

Parris K. M. & McCarthy M. A. (1999a) What influences the structure of frog assemblages at forest streams? *Australian Journal of Ecology* **24**, 495-502.

Parris K. M. & McCarthy M. A. (1999b) What influences the structure of frog assemblages at forest streams? *Austral Ecology* **24**, 495-502.

Perret N., Pradel R., Miaud C., Grolet O. & Joly P. (2003) Transience, dispersal and survival rates in newt patchy populations. *Journal of Animal Ecology* **72**, 567-75.

Petit S., Haysom K., Pywell R., Warman L., Allen D., Booth R. & Firbank L. (2003) Habitat-based models for predicting the occurrence of ground-beetles in arable landscapes: two alternative approaches. *Agriculture, Ecosystems & Environment* **95**, 19-28.

Pyke G. & White A. W. (2000) Factors influencing predation on eggs and tadpoles of the endangered Green and Golden Bell Frog *Litoria aurea* by the introduced Plague Minnow *Gambusia holbrooki*. *Australian Zoologist* **31**, 496-505.

Pyke G. H. (2002) A review of the biology of the Southern Bell Frog *Litoria raniformis* (Anura: Hylidae). *Australian Journal of Zoology* **32**, 32-48.

Quinn G. P., Hillman T. J. & Cook R. (2000) The response of macroinvertebrates to inundation in floodplain wetlands: a possible effect of river regulation? *Regulated Rivers-Research & Management* **16**, 469-77.

Reich R. M., Joy S. M. & Reynolds R. T. (2004) Predicting the location of northern goshawk nests: modelling the spatial dependency between nest locations and forest structure. *Ecological Modelling* **176**, 109-33.

Roberts J., Chick A., Oswald L. & Thompson P. (1995) Effect of carp, *Cyprinus carpio* L, an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. *Marine and Freshwater Research* **46**, 1171-80.

Sainty G. R. J. S. W. L. (2003) *Waterplants in Australia*. Sainty and associates, Sydney.

Semlitsch R. D. (2000) Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* **64**, 615-31.

Skelly D. K. (2001) Distributions of Pond-Breeding Anurans: an Overview of Mechanisms. *Israel Journal of Zoology* **47**, 313-32.

Skelly D. K., Yurewicz K. L., Werner E. E. & Relyea R. A. (2003) Estimating decline and distributional change in amphibians. *Conservation Biology* **17**, 744-51.

Smith M. A. & Green D. M. (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* **28**, 110-28.

Smith M. A. & Green D. M. (2006) Sex, isolation and fidelity: unbiased long distance dispersal in a terrestrial amphibian. *Ecography* **29**, 649-58.

Spencer C., Robertson A. I. & Curtis A. (1998) Development and testing of a rapid appraisal wetland condition index in south-eastern Australia. *Journal of Environmental Management* **54**, 143-59.

Trenham P. C., Koenig W. D. & Shaffer H. B. (2001) Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. *Ecology* **82**, 3519-30.

Vos C. C. & Chardon J. P. (1998) Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology* **35**, 44-56.

Vos C. C. & Stumpel A. H. P. (1996) Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). *Landscape Ecology* **11**, 203-14.

Warwick N. W. & Brock M. A. (2003) Plant reproduction in temporary wetlands: the effects of seasonal timing, depth, and duration of flooding. *Aquatic Botany* **77**, 153
67.

Wassens S. (2008) Review of the past distribution and decline of the southern bell frog *Litoria raniformis* in New South Wales. *Australian Zoologist* **34**, 446-52.

Wassens S., Roshier D. A., Watts R. J. & Robertson A. I. (2007) Spatial patterns of a Southern Bell Frog (*Litoria raniformis)* population in an agricultural landscape. *Pacific Conservation Biology* **13**, 104-10.

Wassens S., Watts R. J., Jansen A. & Roshier D. (2008) Movement patterns of Southern Bell Frogs (*Litoria raniformis*) in response to flooding. *Wildlife Research* **35**, 50 -8.

List of tables

Table 1. Comparison of habitat variables at sites were *L. raniformis* was absent and present. Survey results are pooled for both survey periods (the summers of 2001/2002 and 2003/2004). Prelim main effects give the -2 log likelihood and significance values for the single variable logistic regressions. The higher the -2 log likelihood value the greater the level of unexplained information after the model is fitted.

Table 2. Summary of multivariable backwards stepwise regression, table shows the Nagelkerke R-Square (R^2), the maximum log likelihood ratio (-2Log likelihood), the Hosmer and Lemeshow test (evaluating the fit of the model through a chi-square statistic χ^2, the model fits if the significance value, $\alpha > 0.05$, i.e. the model prediction is not significantly different from the actual observation). The classification table shows the percentage of correct predictions of the absence/presence of *L. raniformis* by the model versus the observed presence/absence of *L. raniformis*. 2003/2004). Refer to Table 1 for explanation of the variable codes.

Table 1. Comparison of habitat variables at sites were *L. raniformis* was absent and present. Survey results are pooled for both survey periods (the summers of 2001/2002 and 2003/2004).

Description	CODE	Mean (±SE)		T-test		Prelim main effects	
		Absent	**Present**	**t**	**p**	-2 Log likelihood	**Sig**
Number of layers of aquatic vegetation	LAY_AQU	1.35 (0.11)	2.51 (0.29)	-4.30	<0.0001	54.508	0.002
Mean height of vegetation (cm)	HEIGHT	13.29 (3.70)	37.59 (7.38)	-3.22	<0.0001	60.717	0.008
Number of layers of fringing vegetation	LAY_FRI	1.25 (0.11)	1.99 (0.24)	-3.14	<0.0001	61.192	0.006
Turbidity	NTU	86.37 (11.42)	45.44 (8.25)	2.60	0.01	61.034	0.024
Water temperature	TEMP (C)	22.54 (0.72)	24.81 (0.48)	-2.36	0.02	64.495	0.030
pH	PH	8.38 (0.11)	7.97 (0.15)	2.25	0.03	65.022	0.370
Conductivity (mScm-1)	CONDUC	1.34 (0.52)	0.27 (0.04)	1.70	0.10	63.760	0.146
Water depth (cm)	DEPTH	34.93 (4.23)	40.45 (2.24)	-1.01	0.32	69.125	0.317
Log wetland area (ha)	AREA	1.43 (0.14)	1.59 (0.12)	-0.82	0.42	69.469	0.414
% cover aquatic vegetation	COV_AQU	47.55 (6.63)	41.30 (8.07)	0.60	0.55	69.780	0.543
% cover fringing vegetation	COV_FRI	75.54 (5.29)	70.68 (6.97)	0.57	0.58	69.825	0.567
Hydrology	HYDRO	categorical				70.045	0.743
Habitat	HABITAT	categorical				69.455	0.406
Hydrology x Number of layers of aquatic vegetation	HYDRO x LAY_AQU	interaction				51.576	0.001

					Hosmer & Lemeshow test		Classification table % accuracy	
Step	Variables included in the model	AIC	R2	2Log likelihood	χ^2	α	Absent %	Present %
1	HYDRO by LAY_AQU+ LAY_AQU +LAY_FRI + HEIGHT+TEMP+ NTU	52.7197	0.697	31.506	2.552	0.959	83.9	80.0
2	HYDRO by							

Prelim main effects give the -2 log likelihood and significance values for the single variable logistic regressions. The higher the -2 log likelihood value the greater the level of unexplained information after the model is fitted.
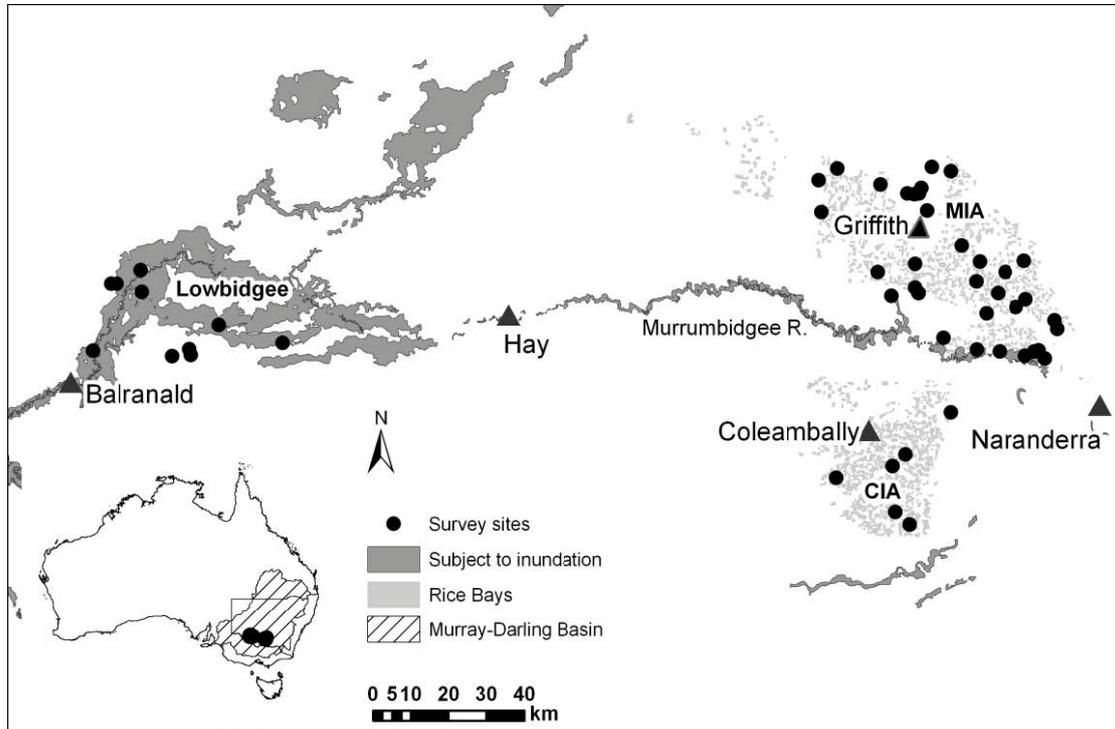
Table 2. Summary of multivariable backwards stepwise regression, table shows the Akaike Information Criterion (AIC) (lower values for AIC indicate a more parsimonious model), Nagelkerke R-Square (R^2), the maximum log likelihood ratio (-2Log likelihood), the Hosmer and Lemeshow test (evaluating the fit of the model through a chi-square statistic χ^2, the model fits if the significance value, $\alpha > 0.05$, i.e. the model prediction is not significantly different from the actual observation). The classification table shows the percentage of correct predictions of the absence/presence of *L. raniformis* by the model versus the observed presence/absence of *L.*

Description	CODE	Mean (±SE)			T-test	Prelim main effects	
		Absent	Present	t	p	-2 Log likelihood	Sig
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% cover aquatic vegetation	COV_AQU	47.55 (6.63)	41.30 (8.07)	0.60	0.55	69.780	0.543
% cover fringing vegetation	COV_FRI	75.54 (5.29)	70.68 (6.97)	0.57	0.58	69.825	0.567

raniformis. Refer to Table 1 for explanation of the variable codes

Figure 1. Location of *L. raniformis* survey sites within inland NSW. Location of *L. raniformis* survey sites within inland NSW. CIA is Coleambally Irrigation Area, MIA is Murrumbidgee Irrigation Area.
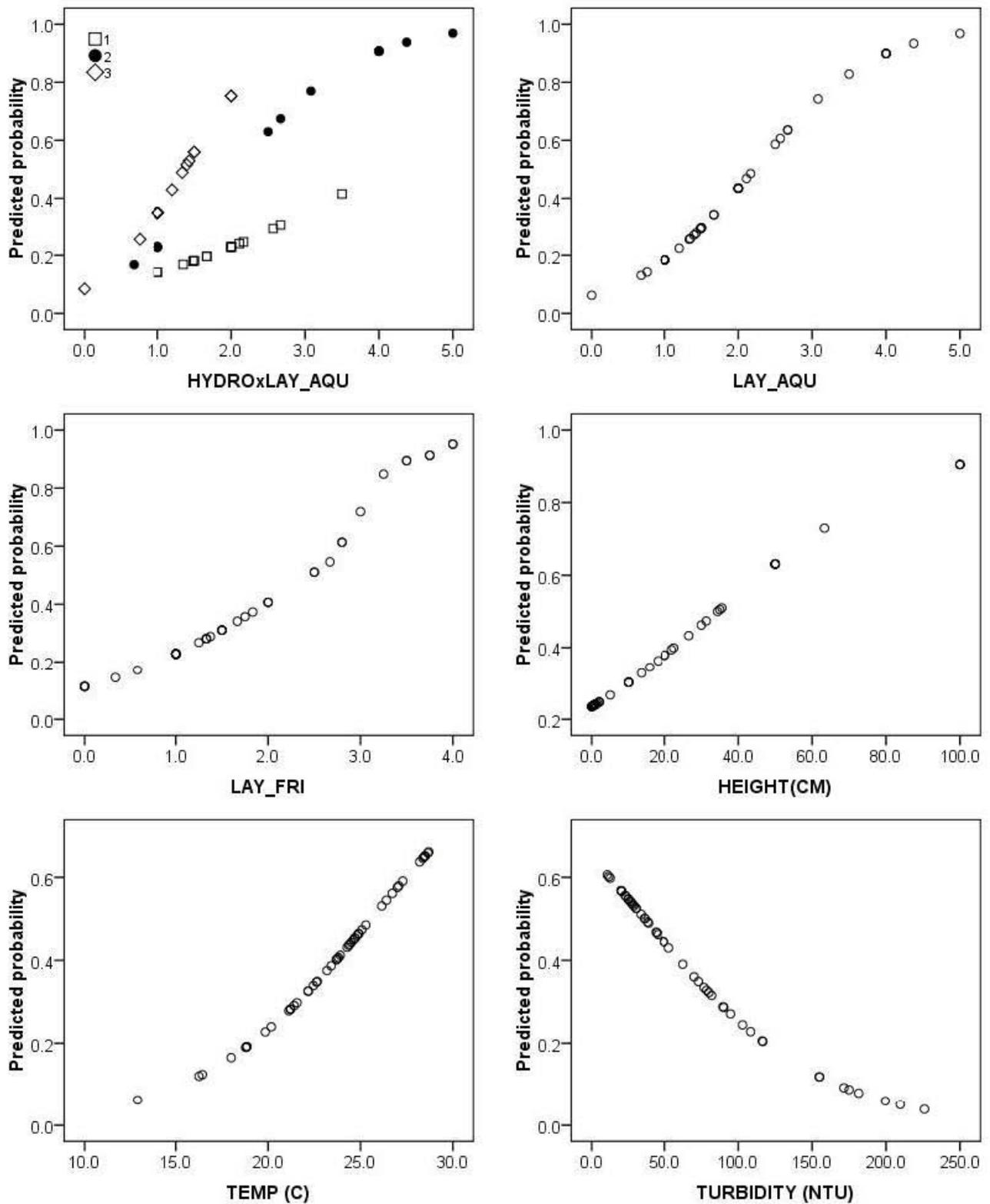
Figure 2. Modelled probability of occupancy by *L. raniformis* based on the selected logistic regression results. **1**. Ephemeral wetlands, **2.** Seasonally flooded wetlands, **3.** Permanent waterbodies. Refer to Table 1 for descriptions of parameter codes.