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THE RELATIONSHIP AMONG MULTIPLE-SCALE HABITAT VARIABLES AND POND USE BY ANURANS IN NORTHERN NEW SOUTH WALES, AUSTRALIA

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***Abstract*.—We assessed the relationships between anuran use and habitat characteristics at 93 ponds. We recorded pond-scale (within 100 m) and landscape-scale (within 500 m) habitat variables and used a generalized linear model framework to determine which variables, if any, related significantly to total anuran abundance, species richness, and the presence and/or abundance of individual species. We recorded 33 species and modeled the distributions of nine. Species richness increased with increasing emergent vegetation and the presence of sandstone, and decreased as the Prescott Index (a measure of ground moisture), elevation, and latitude increased. Total anuran abundance increased with increasing emergent vegetation and pond area and decreased with elevation, pond density, and the Prescott Index. No consistent patterns were evident in the variables showing significant relationships with the presence and/or abundance of individual species. The variables most commonly found to relate to the presence/abundance of individual species were pond shading (appeared in models for eight species) and tree height (six species). Models explained up to 64% of the deviance for presence-absence and 48% for abundance, but usually explained < 35% deviance. Local scale variables were slightly more prevalent in models, but did not obviously have greater influence on the species studied. There was no pattern evident based on phylogeny. Managing species in these forests will need to consider multiple scales and multiple features of the environment.**

Key Words.—anuran; breeding habitat; multiple-scale; pond

INTRODUCTION

It is a long-held evolutionary theory that the distribution and abundance of animals can be determined by their relationship with elements of the environment in which they live (eg. Grinnell 1917). Elements of the environment provide essential requirements in terms of food, shelter, and opportunities for social interactions and the presence/absence or extent of any one element can thus determine whether a species is present and can thrive within an area (Schoener 1974). Understanding the relationships of species with their environment is an important step in providing a platform for their long-term management and has been an area of considerable research and discussion over the last few decades (eg. Morrison et al. 2006).

Understanding the habitat relationships of anurans is of particular importance due to their dual aquatic and terrestrial life-cycles and numerous studies have provided indications that the presence and abundance of anurans at breeding sites is likely influenced by a number of abiotic and biotic factors. The former includes temperature (Pope et al. 2000; Di Mauro and Hunter 2002), hydroperiod (Lehtinen et al. 1999; Beja and Alcazar 2003; Watson et al. 2003), water quality (Banks and Beebee 1987; Stumpel and Van Der Voet 1998) and the latter vegetation structure in and around the pond (Pavignano et al. 1990; Munger et al. 1998; Vos and Chardon 1998; Bosch and Martinez-Solano 2003). These studies have demonstrated that the features associated with the use of breeding sites by anurans vary considerably between species and habitats and are related to the pond or the habitat immediately surrounding the pond. Features of the surrounding environment (eg. forest structure) are more likely to be directly influenced by human land-use practices and so are ones that may be protected through management practices.

Importantly, there has been recent recognition of the role of “complementary habitat” in determining the use of breeding sites by species (Pope et al. 2000; Guerry and Hunter 2002). Many species only use breeding sites that have specific adjacent or nearby non-breeding habitats (eg. Lamoureux and Madison 1999; Pope et al. 2000; Pilliod et al. 2002). These complementary non-breeding habitats usually occur within migration distance of the breeding site and provide summer feeding and shelter sites and/or critical overwintering sites (Semlitsch 2000; Semlitsch and Bodie 2003). Hence, investigations of the associations of anurans and breeding sites need to consider the associated surrounding habitat if a proper understanding of the role of habitat is to be attained

Studies of the relationships between habitat and pond use by anurans in Australian pond systems have covered different habitats and provided varying results. In riverine floodplains, species richness and total anuran abundance are positively related to number of riparian plant species, but not to water quality, and each species associated with a different set of riparian plants (Healey et al. 1997). Comparisons of anurans using montane natural and artificial ponds found a positive relationship between canopy cover and total species richness (Hazell 2003). The extent of bare ground around a pond and emergent vegetation at the water's edge also correlated with pond use for several species. Further work suggested high species richness was associated with greater levels of emergent vegetation and the absence of fish (Hazell et al. 2004). Species richness and anuran abundance at artificial ponds located in upland forested areas can be positively or negatively influenced by altitude, latitude, rainfall, forest wetness, and extent of dry forest (Lemckert 1999). Species richness and abundance of anurans at ponds in mid-altitude sites relate to a wide range of habitat variables (Lemckert et al. 2006), which include water depth, amount of emergent and surrounding vegetation cover, and degree of grass in the surrounding ground cover. The relationships varied between each species and in the direction of influence (+ve or –ve) between species. However, the importance of broader scale habitat features has received little attention in any of these studies.

An understanding of why anurans use particular breeding sites is valuable for their management and conservation. Identifying pond types that contribute more to anuran diversity or are used as breeding sites for endangered species can lead to the preferential protection of breeding sites and the creation of suitable breeding habitat. Considering the recent and increasing dramatic global (Blaustein and Wake 1990; Tyler 1991; McCallum 2007; Wake and Vredenburg 2008) and local (see Tyler 1991; Pechmann and Wilbur 1994) decline of amphibians, retaining or providing high quality breeding habitat is a major conservation objective, ensuring high levels of recruitment to leave populations more robust to natural or artificial perturbations.

We searched for relationships between pond use by anurans and a series of habitat characteristics associated with those ponds, exploring which factors relate to the numbers of anurans and species using the ponds. We were interested if specific habitat features are associated with increased anuran presence or abundance and if there was any consistency in this association over multiple species. We also wanted to assess if habitat features measured at a broader scale may better discriminate pond use. This would suggest that complementary habitat features may have a significant determinant role in this system and also suggest if broader scales need to be considered for managing these anuran populations. Finally, we were interested if phylogenetic patterns are evident in the features showing significant relationships with pond use by anurans.

MATERIALS AND METHODS

***Study site.*—**We studied 93 ponds located in forested areas along a 500 km strip between the central and mid-north coastal areas of New South Wales (NSW), Australia (Fig. 1). The ponds clustered into four broad regions: the Central Coast, Bulahdelah, Wauchope, and Dorrigo areas. The lands represent a series of coastal mountain ranges with maximum elevations of approximately 400 m in the south to over 1000 m in the north. Rainfall is variable, but is a mean of approximately 1300 mm and a maximum of over 2600 mm in the northern areas. Temperatures are mild, with a mean minimum of 6.3° C (July) and mean maximum of 27.5° C (January). The ponds studied occur in areas of predominantly intact native forests that vary from temperate rainforests to dry open hardwood forests, but dry eucalypt forests predominate (Harden 1991). Commercial logging throughout this region commenced early in the last century and has increased in intensity with mechanization, particularly during and after the 1940s.

The ponds examined in this study are human-constructed for fire fighting and stock watering. Most ponds were located within tracts of forest, but a few ponds on the edge of these forests had some degree of clearing of the surrounding vegetation. At least 65% of the land within a 500 m radius of all ponds was covered by native vegetation.

***Survey methods.*—**The variety and numbers of anurans using each pond were measured through counts undertaken between the 1 September 2001 and 30 April 2006. During this period ponds were surveyed a minimum seven times, but most (> 75%) were searched more than 12 times. We searched between 1900 and 0200, dependent on the season and time of sunset, but with 90% of searches being performed within three hours of sunset. On each occasion, we listened for an initial 3–5 minute period to record calling males, followed by a visual search of the pond and the adjacent 20 m section of bank to locate non-calling anurans (5–20 minutes of searching). Exact counts of some of the smaller species when in large choruses were not possible, and consequently numbers were estimated to the nearest multiple of 10. We recorded the number of species, number of calling individuals, time, date, and weather conditions. We visited ponds at random and eight to 10 ponds were searched on any given night. This minimized the influence of any temporal (nightly cycle) and/or environmental (weather change) patterns in the analysis. The broad spread of survey times allowed us to cover a range of micrometeorological conditions and ensure that at least two surveys of each pond were undertaken after significant rainfall events (> 10 mm in the previous 24 hours).

We recorded 23 habitat variables associated with each pond (Table 1), and chose those most likely to be

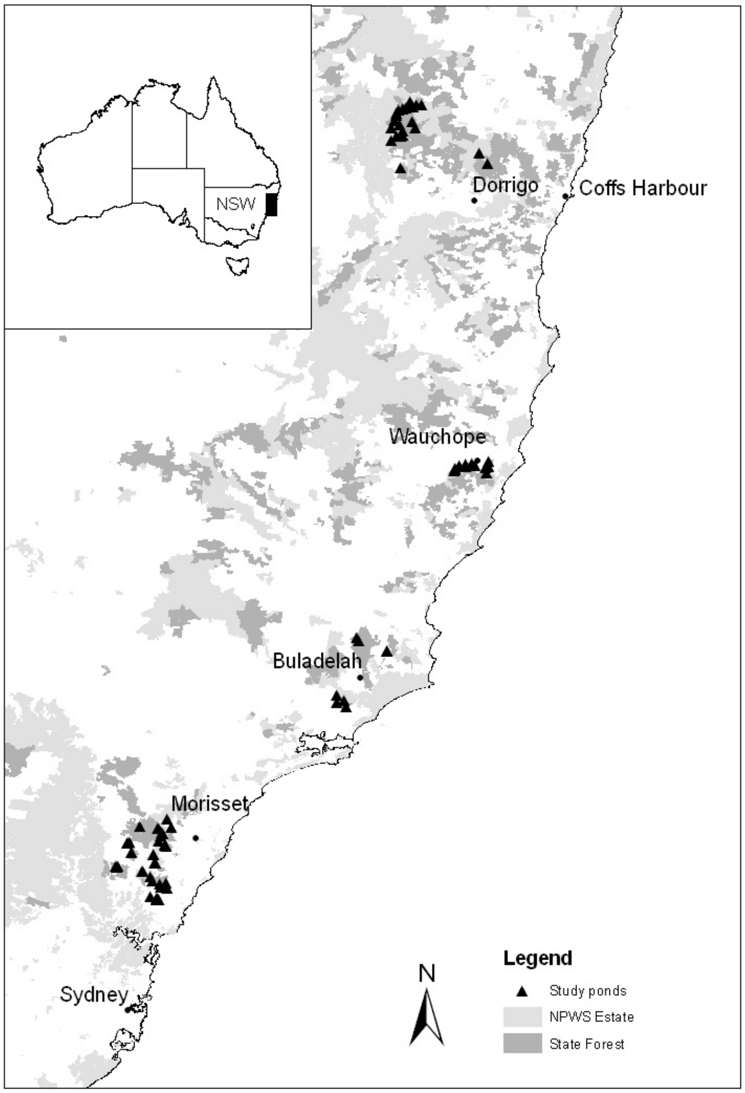

FIGURE 1. The location of the pond sites in New South Wales, Australia that we used in this study.

important based on previous studies and our own field observations. These variables, hereafter referred to as pond-scale variables, can be divided into features of the breeding site itself and features of the habitat available around the breeding site. The former indicates features that may be important for an anuran in selecting a suitable breeding site. The latter indicates habitat features that may be important for calling sites, daytime shelter sites when not calling, foraging habitat, or as non-breeding habitat. We measured the surrounding habitat variables in 5 x 5 m quadrats centered at four points located 55 m from the edge of the pond (each at 90° to the others with the first randomly chosen) and the mean or maximum (for tree and understorey cover) used in the subsequent analyses. We recorded the number of stumps along four 50 x 20 m transects running perpendicular to the pond with the 55 m points as their center points. The distance of 55 m was chosen to represent the habitat adjacent to the pond that we considered anurans attending to reproduce would use for calling and/or shelter during the period of their stay. This number is to a degree arbitrary, but is based on personal experience and work from studies such as Lemckert and Slatyer (2002) and Penman et al. (2005).

We also obtained data on 10 broader scale Geographic Information System (GIS) derived variables and added them to the analyses (Table 2). We based the variables, hereafter referred to as landscape-scale variables, on a 500 m radius around the breeding site and provide indications as to whether still broader-scale habitat measures might influence pond-use by anurans. We chose 500 m based on the findings of Lemckert (2004) that indicated individuals using ponds rarely moved more than 300 m from ponds and so 500 m provides a distance that should lead to independent populations. The Prescott Index (Prescott 1948) provides a measure of the relative

TABLE 1. Variables used in the analyses of pond breeding anurans in Australia and their categorization. Those in italics relate directly to features of the breeding pond and the others to the habitat surrounding the breeding site. Variables marked with an * were used in the final modeling process.

Variable	Categories
*Depth**	*Continuous (in cm)*
*Area**	*Continuous (in m^2)*
Water Body	*Nominal – Permanent or not*
*%Bare**	*Ratio – % area of bare pond substrate*
*%Emerg**	*Ratio – % of pond covered by emergent vegetation*
*Bankveg**	*Ratio – % of pond bank covered by vegetation*
*%Shade**	*Ratio – % of the pond shaded by vegetation*
Sand*	Nominal – Sand or not sand
Forest	Nominal – Dry or wet
Mixed Age	Nominal – Mixed or even aged forest
Dist.*	Nominal – Recently disturbed (= regenerating) forest or not
Mat*	Nominal – Forest is composed of mainly mature trees or not
Stumps*	Continuous – Mean number of stumps on transect (0.1 ha) or (20 m x 50 m)
Nonfor*	Ratio – % area cleared in a 300 m radius
Mean-Fire*	Continuous – Mean height of fire scars
Overst*	Ratio – mean % of canopy cover in surrounding forest
Mean-DbH*	Continuous – Mean diameter at breast height of trees in surrounding forest
Tree Ht*	Continuous – Mean tree height
Rainforest	Nominal – rainforest understorey or no rainforest understorey
Heath	Nominal – Heath in forest or not
Und-Cover*	Ratio – maximum% of understorey cover in surrounding forest
Ground Veg*	Ratio – mean % of vegetation as ground cover
Litter*	Continuous – mean litter depth (cm)

moisture levels present in an area, taking into consideration rainfall and evaporation. Pond density measures the number of other ponds studied that were present within a 500 m radius. Comparing the anurans present at a pond with this variable indicates, by a positive association, that a species concentrates in large numbers where there are several ponds in close proximity rather than where ponds are isolated. Alternatively, the presence of many alternative sites nearby that causes the available males to spread out, may dilute the number of anurans calling at a pond. We used a Spatially Lagged Response Variable (SLRV; as defined by Haining 2003) to account for spatial autocorrelation in the response variable (anuran counts). To calculate the SLRV for each pond, we summed the product of the weight and the response for all other ponds within the cluster and divided the score by the sum of the weights. The weighting used in this analysis was the inverse distance between two ponds and the response was the abundance of the species at a pond (Penman et al. 2008). The SLRV score provides an indication as to whether, in a region, a pond with a greater calling male abundance is associated with a similarly large number of calling males at nearby ponds. If so, this indicates that species favor ponds that are clustered within one or several areas of the region, with the other parts of the region having few or no records of that species.

Finally, we included whether a pond was located in the Chaelundi region or not as an added variable because the number of anurans in this northern region appeared to be larger than in the other regions. Including this variable ensured that the data from Chaelundi sites did not dominate the analysis.

***Analyses.*—**We analyzed only a subset of all the species recorded. We removed “explosive” breeding species because we could not obtain counts for all sites under similar conditions, particularly during heavy rainfall events when explosive breeders are most detectable. We also removed species known to prefer breeding in running streams because it was unclear as to what their presence at a pond indicated as they were generally not recorded calling.

We elected to use the maximum counts obtained per site in the analyses, rather than the mean count, because of the highly variable nature of anuran counts, particularly the very high numbers that can be recorded when climatic conditions are optimal. We surveyed some sites five or six times during good conditions and some only once or twice; therefore, the latter sites would have lower mean counts simply because of survey chance. We were able to survey each site at least twice in what our experience were optimum conditions (warm nights after rainfall) and so the maximum count should provide a more even comparison of the relative abundance of anurans between the study ponds.

We created a Spearman rank matrix and assessed the correlations between variables. Where strong correlations were evident, we retained the variable we considered most likely to have an obvious biological meaning (expert selection) and was preferably independent. We used Canonical Correspondence Analysis and reduced this set to include only variables that provided significant explanatory power based on their ordinations. This process reduced the final analysis to 18 pond-scale variables, 11 landscape-scale

TABLE 2. Landscape based variables used in analyses of pond breeding anurans in Australia.

Aspect	Aspect (majority over 500 m buffer)
Elev	Elevation (height above sea level)
North	Latitude
Sandst	Majority value – sandstone vs other bedrock type
Solar	Mean Solar Radiation (low to high)
Wetness	Mean Wetness (wet to dry)
Pres (Prescott Index – see text)	Water balance (wet to dry)
Dens (Pond density – see text)	Number of ponds in forest within 500 m
SLVR (see text)	Relative clustering of frogs within regions
Topo	Topographic position low to high

variables and the Chaelundi dummy variable (Tables 1 and 2).

We adopted an information theoretic approach to model building. For both the binomial and Poisson components of the model, we manually inserted and removed variables, testing all combinations of models including up to x variables, where x is the number of sites/10 (after Wintle et al. 2005). We retained variables in a model if they were significant at $\alpha = 0.05$ level and if they significantly reduced the model fit, as tested by Akaikes Information Criteria (Akaike 1973). We used the terminology of Burnham and Anderson (2001), where models with 2 AIC points have strong support, those with four and seven have some support and those greater than 10 having essentially no support.

We explored the relationships between total number of species and the total number of anurans counted at each pond using a generalized linear model (GLM) framework. Initially we plotted the 30 variables against the counts to determine visually which showed some relationship with richness or total abundance. The model fitting was then a manual iterative process with each parameter (environmental variable) being included in the model until all possible combinations had been considered. The final model chosen was that showing the greatest amount of explanatory power and with all of the included parameters being significant at $\alpha = 0.05$.

For individual species' responses, we assessed any species recorded at 20% or more of the ponds, as presence levels less than this produced unstable models. Suitable variables (significant at the $P < 0.05$ level) were included either in a GLM with a Poisson distribution (where species were present > 60 sites) or in a zero-inflated Poisson (ZIP) regression modeling process. We considered a ZIP model essential due to the large number of zero counts for each species (Welsh et al. 1996). In this process, a mixture model of zero point mass (logistic) and a Poisson distribution was assumed. We allowed covariates to enter in both processes. Parameters were fitted using maximum likelihood techniques for the mixture distribution. Again, we calculated the models with all possible combinations and we selected the model that provided the best explanatory power and with all retained parameters being significant ($\alpha = 0.05$). To assess for possible phylogenetic patterns, we split and tabled the species into the two families and looked for similarity in the significant variables recorded for each species. All analyses were conducted using the R-package version 2.7.1 (R-Development Core Team 2008) in association with the VEGAN library (Oksanen et al. 2005.

RESULTS

We recorded 33 species of anurans during the course of the study. The mean number of anurans recorded per pond was seven with a range of 1–12. We recorded six species at more than 50 of the study ponds and 12 species at 10 or fewer ponds. We removed explosive and stream breeders, and used the remaining 14 species in the analysis. The myobatrachids *Crinia signifera* (63 ponds) and *Limnodynastes peronii* (73 ponds) and the hylid *Litoria peronii* (83 ponds) were the most regularly recorded species.

The number of species present at a site was significantly related with the Prescott Index (Estimate = -0.149, $t = 4.42$, $P < 0.001$), % emergent vegetation (Estimate = 0.036, $t = 3.10$, $P < 0.005$), sandstone (Estimate = 3.936, $t = 3.01$, $P < 0.005$), elevation (Estimate = -0.005, $t = 3.18$, $P < 0.005$), and northing (Estimate = 0.001, $t = 2.55$, $P < 0.05$). That is, ponds with greater numbers of species were those generally with more emergent vegetation, found on sandy soils, located in dryer forests, at lower altitudes, and in the north of the study area. The total deviance explained was 39%.

Total anuran abundance was also significantly related to the Prescott Index (Estimate = -0.153, $t = 3.44$, $P < 0.001$), % emergent vegetation (Estimate = 0.068, t = 4.29, $P < 0.005$), elevation (Estimate = -0.003, $t = 2.29$, $P < 0.05$), pond area (Estimate = 0.002, $t = 2.37$, $P < 0.05$), and pond density (Estimate = -1.468, $t = 3.00$, $P < 0.005$). Again, this means that ponds with greater numbers of anurans were associated with dryer forest environments, had more emergent vegetation, were at lower altitudes, were larger, and were unlikely to have many other ponds nearby. The total deviance accounted for by the model was 33%.

A broad range of variables related with the presence/absence and or abundance of the different

TABLE 3. Significant environmental variables showing relationships with the presence/absence and abundance of hylid species. Number of sites occupied by each species is listed below the species name, followed by the deviance explained by the model presented. Est = estimate and SE = standard error. Landscape scale variables are bolded

Species	Logistic distribution	Poisson distribution
Litoria fallax N = 60; 51% & 26%	**Elev (Est = -0.008; SE = 0.002; P < 0.01)**, **Solar (Est = 1.812; SE = 0.621; P < 0.01)**	Bare (Est = -0.014; SE = 0.001; P < 0.001), Shade (Est = -0.029; SE = 0.003; P < 0.001), Tree Ht (Est = 0.032; SE = 0.004; P < 0.001), **SLRV (Est = 0.011; SE = 0.001; P < 0.001)**, **Elev (Est = -0.002; SE = 0.000; P < 0.001); Solar (Est = 0.376; SE = 0.078; P < 0.001)**
Litoria latopalmata N = 38; 14% & 28%	Shade (Est = -0.065; SE = 0.023; *P* < 0.005), Tree Ht (Est = -0.120; SE = 0.043; P < 0.01), **Solar (Est = -1.304; SE = 0.482; P < 0.01), Pres (Est = -0.091; SE = 0.039; P < 0.05)**	Nonfor (Est = -0.013; SE = 0.003; P < 0.001)
Litoria peronii N = 83; 43%	NA	Nonfor (z = -8.26; P < 0.001), Shade (z = -8.93; P < 0.001), Tree Ht (z = 5.79; P < 0.001), Dist (z = -2.21; P < 0.05), **Pres (z = -7.77; P < 0.001), Elev (z = -8.31; P < 0.001)**
Litoria tyleri N = 39; 64% & 15%	Bare (Est = -0.017; SE = 0.008; P < 0.05), **SLRV (Est = 0.103; SE = 0.038; P < 0.01)**	Nonfor (Est = -0.010; SE = 0.003; P < 0.005), Tree Ht (Est = 0.053; SE = 0.015; P < 0.001), Shade (Est = -0.054; SE = 0.008; P < 0.001), Bare (Est = -0.010; SE = 0.002; P < 0.001), **Pres (Est = 0.023; SE = 0.010; P < 0.05), SLRV (Est = 0.039; SE = 0.005; P < 0.001), Dens (Est = 0.152; SE = 0.008; P < 0.05)**

species and each species had multiple variables related with either their presence/absence or abundance. Shading level of the pond was significant for eight of the nine species and was included as a significant variable in 10 models (three presence/absence and seven abundance models), eight of which showed a negative relationship. Tree height was significant in seven models (two presence/absence) covering six species, but varied between species as to the relationship. The solar index and SLRV were both found to be significant in six models (three and two presence/absences models respectively) covering four species each, but not exactly the same species. The relationships with SLRV were always positive, but the solar index varied in its direction of relationship.

The amount of deviance explained by the models varied from a high of 64% for the presence/absence model for *Litoria tyleri* to a low of 14% for the presence/absence model for *Litoria latopalmata*. Models generally explained between 20 and 45% of the deviance in the data. Notably, whilst the presence/absence model for *Litoria tyleri* provided good explanatory power, abundance only explained 15% of the deviance seen in the data. Therefore, the model may be able to predict relatively well where this species will be found, but provides little indication of whether it would be abundant at a site. The levels of deviance explained were much more consistent between presence/absence and abundance for the other species modeled in this manner.

In the presence models produced, pond-scale variables accounted for eight of the 17 variables modeled to be significant. In modeling abundance, 26 of 42 significant associations were pond-scale variables. Ten of the 18 pond-scale variables available for the final modeling process were not included in any of the final models: depth, bankveg, sand, stumps, mean-fire, overst, mean-dbh, und-cover, litter (see Table 1 for variable codes). Pond area only appeared once in the total anuran abundance model. Of the landscape-scale variables, aspect and topographic position were not significant in any model and northing, sandstone, wetness, and Chaelundi just once.

Ten different variables appeared in the significant relationships found for the four hylid species modeled. This contrasts with the 15 different variables appearing as significant for the five myobatrachids modeled. In terms of the presence and absence modeling, we recorded eight significant relationships including seven variables for the hylids compared to nine significant relationships including eight variables for the myobatrachids. The abundance of the hylid species showed 19 significant relationships covering 10 variables compared with 23 significant relationships covering 13 variables for the myobatrachids. That is they covered roughly similar numbers of variables in both categories given the presence of an additional myobatrachid species. Shading was significant in four of the seven hylid models produced and six of the nine myobatrachid models. Tree height was significant in three of the eight hylid models and four of the nine myobatrachid models.

DISCUSSION

The variables relating to the presence and/or abundance of anuran species at these ponds varied widely between species. Equally, the variables relating to the presence of a species could differ greatly from those relating to its abundance at a site.

TABLE 4. Significant environmental variables determining the presence/absence and abundance of myobatrachid species at the ponds. Number of sites occupied by each species is listed below the species name, followed by the deviance explained by the model presented. Est = estimate and SE = standard error. Landscape scale variables are bolded.

Species	Logistic distribution	Poisson distribution
Adelotus brevis N = 31; 34% & 23%	Bare (Est = -0.040; SE = 0.026; P < 0.005), Tree Ht (Est = 0.187; SE = 0.072; P < 0.01), Shade (Est = -0.077; SE = 0.033; P < 0.05), **Pres (Est = 0.091; SE = 0.043; P < 0.05)**	Tree Ht (Est = -0.102; SE = 0.026; P < 0.001), Mat (Est = -1.767; SE 0.501; P < 0.001), Shade (Est = 0.035; SE = 0.011; P < 0.005)
Crinia signifera N = 63; 48%	NA	Dist (z = -7.58; P < 0.001), Shade (z = -5.23; P < 0.001), Nonfor (z = 9.10; P < 0.001), Tree Ht (z = -7.90; P < 0.001), **SLRV (z = 2.14; P < 0.05), Elev (z = 8.58; P < 0.001), Solar (z = -4.89; P < 0.001)**
Limnodynastes peronii N = 73; 21%	NA	Shade (z = 2.72; P < 0.005), Ground Veg (z = -4.52; P < 0.001); Mat (z = -2.37; P < 0.05), **Wetness (z = -5.44; P < 0.001), Dens (z = -5.96; P < 0.001)**
Mixophyes fasciolatus N = 39; 42% & 38%	**Chael (Est = 6.108; SE = 1.506; *P* < 0.001), Solar (Est = -1.498; SE = 0.711; P < 0.05)**	Ground Veg (Est = 0.017; SE = 0.006; *P* < 0.005), **Solar (Est = 0.821; SE = 0.101; P < 0.001)**
Uperoleia fusca N = 56; 27% & 23%	Shade (Est = -0.054: SE = 0.020; P < 0.01), Emerg (Est = 0.051; SE = 0.016; P < 0.005), **SLRV (Est = 0.097; SE = 0.040; P < 0.05)**	Shade (Est = -0.041; SE = 0.004; P < 0.001), Ground Veg (Est = -0.008; SE = 0.003; P < 0.05), Emerg (Est = 0.004; SE = 0.002; P < 0.05), **Pres (Est = -0.018; SE = 0.004; P < 0.001), SLRV (Est = 0.011; SE = 0.003; P < 0.001), Dens (Est = -0.118; SE = 0.035; P < 0.005)**

The pond and landscape scale variables appeared to be equally likely to provide a significant relationship and there was no obvious pattern of “important” factors when phylogeny was considered.

We had expected that specific habitat features would regularly show a significant relationship with either the presence or abundance of species, but only shading of the pond showed a consistent relationship with the distributions of species. We expected a negative relationship with shading as this reduces water temperatures, which reduces the relative fitness of tadpoles (Skelly et al. 2002; Lauck et al. 2005) and pond use by amphibians (Skelly et al. 1999). In our study, the presence and/or abundance of six species was negatively associated with shading. The two species showing a positive relationship with increasing shading, *Adelotus brevis* and *Limnodynastes peronii*, both call and lay egg masses under cover on the edges of ponds (the other species do not) and shaded ponds appear to provide more cover at the pond margins. Presumably, their tadpoles are better able to cope with reduced water temperatures compared to the other species in this study, but this has not been empirically confirmed. Tree height was important for six species and was not uniform in the direction of the relationship. There is little obvious consistency in the types of habitat variables that relate to pond use.

The irregular pattern evident in the relationships between anurans and habitat variables follows the findings of other studies on Australian anurans (Healy et al. 1997; Hazell et al. 2001;Lemckert et al. 2006). This result suggests that habitat partitioning may be taking place to minimize competition, with each species adapting into its own niche. Such an approach would reduce competition for resources and suggest that autecology may play the major role in determining pond use. This area needs further consideration and testing.

We assessed if understanding habitat characteristics at a landscape scale may provide better insights into pond use by anurans. A number of authors have noted the importance of having suitable complementary habitat within migration distance of a breeding pond (eg. Lamoureux and Madison 1999; Pope et al. 2000; Pilliod et al. 2002). Most of the work assessing habitat influences on pond use has investigated only relatively fine scale variables such as pond structure or vegetation immediately surrounding the breeding site, generally within 50 m. Research has indicated that anurans are likely to migrate to non-breeding habitats between 50 to 200 m (reviews by Semlitsch and Bodie 2003; Lemckert 2004), and the roles of these important nearby habitats in determining pond use have not frequently been assessed. Neither scale (55 m or 500 m radius) of habitat measurements appeared to dominate in our models. Local scale factors may have been slightly more prevalent in relating to abundance models for individual species, but only slightly so. Both pond and landscape-scale features of the habitat are likely to have some role in influencing pond use and need to be considered when managing the environment. The pond and its immediately adjacent habitat cannot be considered in isolation.

The relatively large number of pond sites and habitat variables available in this study resulted in models that were able to explain large proportions of the observed deviance (compared to Lemckert et al. 2006). This latter study included one of the four areas included in this study, but was limited to 45 ponds and included no landscape scale variables. Increasing the number of ponds used in habitat assessments increased the explanatory power and several models approached or exceeded 50% explanatory power, which is relatively large for such studies. Such levels begin to provide managers with strong indications of the habitat features that may be of importance for the presence and abundance of a species and so provide useful management directions.

Some amphibian populations may be structured as metapopulations (e.g., Sjogren 1991; Hecnar and M'Closkey 1997; Pope et al. 2000; Marsh and Trenham 2001) and this has been the case for Green and Golden Bell Frogs (*Litoria aurea*) in Australia (Goldingay and Lewis 1999; Hamer and Mahony 2007). Hence, we were interested to see if there was any evidence for a possible metapopulation structure in this study, although we do recognize the concerns of the way metapopulation is used in describing anuran populations (Smith and Green 2006. We expected strong and regular positive relationships with the SLRV. This should occur if there is a strong clustering of occupied sites with high abundance. The close proximity of occupied sites would facilitate the required movements and interactions of individuals between these ponds in order to allow metapopulation processes to work. SLRV showed a significant relationship with calling in six models covering four species and was positive in each case, suggesting some clustering of anurans in regions, but this was not a widespread relationship. In addition, we would expect that increased pond density would better allow metapopulations to exist. The availability of clusters of ponds within close proximity would provide a situation where metapopulation-driven species can establish breeding populations in multiple ponds that can interact to produce a single robust metapopulation. Clusters of ponds did occur in the different regions, but this did not result in increased densities of individual species at the ponds found in clusters compared to ponds that were more isolated.

Predation can be important in structuring populations and communities of amphibians and needs consideration in this system. Fish can be an important determinant of pond use (Bradford et al. 1993; Hazell et al. 2004; Knapp 2005), but we did not observe fish in any of the ponds even when at very low water levels when any fish present would have been evident. Hence, they could not influence the populations in this study. Invertebrate predators may also influence anuran recruitment, but we did not measure their presence and abundance. There is little evidence available to indicate whether invertebrates may play a strong structuring role in any Australian anuran system, although Richards and Bull (1990) did find odonates to be capable predators on tadpoles. However, we believe that the relatively uniform environments and pond constructions minimize differences in invertebrate assemblages or abundances and so do not exert enough influence to produce the variable results evident. We acknowledge however, that this is an area requiring further study.

We note that pond hydroperiod, which has been found to be a very important factor in amphibian presence and abundance overseas (e.g. Lehtinen et. al. 1999; Beja and Alcazar 2003; Watson et. al. 2003) was removed early from our analyses as a co-correlated variable. Our study ponds are almost all essentially permanent, except in times of very severe drought, when all may dry out. Hence, hydroperiod should not account for the differences seen between many of the ponds.

We wanted to determine if there were particular aspects of a pond that would make it more suitable for a greater variety and number of anurans. However, no one measured feature strongly related to greater numbers of species or total abundances of anurans using a pond. Rather, each species had a unique group of attributes that were associated with anuran presence or abundance. Building a pond with specific attributes may positively influence some species, but provide a poor breeding site for other species. Maintaining a diversity of species and large numbers of anurans in this region is dependant on maintaining a variety of ponds with different shapes, sizes, and surrounding vegetation conditions. However, it is equally important to consider the broader location of a pond in the landscape to ensure that there is a range of ponds in a range of different habitats. These varying habitats provide the critical complementary non-breeding habitat for the anurans to use and so make a pond a viable breeding site.

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FRANCIS LEMCKERT, everyone calls him Frank, began his career in biology by undertaking a B.Sc. in Zoology at the University of Sydney. He followed this with a M.Sc. looking at the population dynamics of *Crinia signifera*, also at the University of Sydney, before accepting a position as a research scientist with the Forestry Commission of New South Wales in 1995. Frank has remained working within the government since that time, directing his energies into the conservation of forest fauna, with a specific interest in the ecology and management of forest dependent frogs. This included both studies of single species ecology and of communities and how the environment influences their composition and abundance. His research interests also include improving anuran survey and monitoring methods, the ecology of threatened reptiles, the use of tree plantings to restore habitat and connectivity in agricultural landscapes, and assessing the value of the Australian National Reserve System in protecting fauna. Frank also regularly runs wildlife survey and identification courses attended by researchers, ecological consultants, and government staff. Frank recently completed his Ph.D. at the University of Newcastle, which considered the management of frogs in the timber production forests of eastern New South Wales, and he is further expanding his work into the management of the herpetofauna of the croplands and rangelands of eastern Australia.

MICHAEL MAHONY is currently the head of the Discipline of Environmental Science and Management at the University of Newcastle, Australia, where he has previously held positions as the head of the discipline Biology and as the Assistant Dean for Research Training in the Faculty of Science and IT. My biological interests and research are somewhat diverse, my doctoral work was in the area of cytogenetics and genetics of Australian ground frogs (Myobatrachidae and Limnondynastidae) and considered the origins and relationships of polyploidy in the genus *Neobatrachus* along with standard and banding staining of chromosomes of this diverse group. With the occurrence of amphibian declines in the early 1980s in Australia my attention changed its focus to understanding the cause of these declines and developing conservation management strategies. It was in a reciprocal translocation field experiment with a rapidly declining frog species, that the first observations were made of sick and dying frogs in the wild associated with declining species. These observations indicated that a disease was responsible, and consequently the first identification of chytrid fungus was made from the study site. Investigations of the declining frog problem continue with current research directed towards several model species and my laboratory currently has 12 postgraduate students and three postdoctoral researchers working on managing threatened amphibian populations.