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# Amphibian Abundance and Detection Trends During a Large Flood in a Semi-Arid Floodplain Wetland

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*Abstract*.—**Amphibian abundance and occupancy are often reduced in regulated river systems near dams, but comparatively little is known about how they are affected on floodplain wetlands downstream or the effects of actively managed flows. We assessed frog diversity in the Macquarie Marshes, a semi-arid floodplain wetland of conservation significance, identifying environmental variables that might explain abundances and detection of species. We collected relative abundance data of 15 amphibian species at 30 sites over four months, coinciding with a large natural flood. We observed an average of 39.9 ± (SE) 4.3 (range, 0-246) individuals per site survey, over 47 survey nights. Three non-burrowing, ground-dwelling species were most abundant at temporarily flooded sites with low-growing aquatic vegetation (e.g., *Limnodynastes tasmaniensis*, *Limnodynastes fletcheri*, *Crinia parinsignifera*). Most arboreal species (e.g., *Litoria caerulea*) were more abundant in wooded habitat, regardless of water permanency. Remaining species had burrowing frog characteristics and low or variable abundance during the flood (e.g., *Litoria platycephala*, *Uperoleia rugosa*) with no significant environmental covariate influence. Consequently, behaviorally and physiologically similar species shared similar responses, despite some species-specific relationships to site- and survey-level variables. The Macquarie Marshes provided suitable habitat for a range of species with varying adaptations to semi-arid conditions, including those highly susceptible to water loss. It was likely regular inundation and natural flooding patterns were required to maintain these conditions.**

*Key Words.*—abundance modeling; Australia; environmental flows; Hylidae; Limnodynastidae; Macquarie Marshes; Mytobatrachidae; river regulation

## Introduction

Amphibians are conspicuous and important components of wetlands. Most species are closely coupled with freshwater systems due to their low skin resistance to water loss and aquatic larval stage (Wells 2007). Floodplain systems typically contain a mosaic of vegetation types and water bodies with varying hydroperiod lengths that provide amphibians with areas of suitable shelter and breeding conditions. However, the distribution and abundance of amphibians across the floodplain are rarely spatially or temporally uniform. Water bodies within the floodplain with long hydroperiods (inundated for one year or longer) tend to exclude species vulnerable to predators such as fish, whereas wetlands with short hydroperiods exclude species that require extended development times for metamorphosis (Baber et al. 2004). Differences in hydroperiod length and water temperature among water bodies also influence population density of individual species (Indermaur et al. 2010). Disrupted river flows near dams can modify flooding patterns of wetlands and riparian zones, negatively affecting amphibian abundance (Eskew et al. 2012; Kupferberg et al. 2012) and altering amphibian community composition (Wassens and Maher 2011). Wetland systems further downstream of dams are also often highly impacted by river regulation (Kingsford 2000), but little is known about impacts on amphibian communities.

Floodplain wetlands in semi-arid and arid regions (< 500 mm of rain annually, herein Dryland) are sustained by river flows originating from upper catchments, often in more mesic areas. Resulting flood pulses are the shortest temporal unit of the flow regime, representing an annual or seasonal flow event (Walker et al. 1995). These flooding pulses produce an increase in abundance in a range of aquatic animals (Kingsford et al. 1999; Balcombe et al. 2012) and plants (Brock et al. 2006), triggered by high productivity in the aquatic food web (Bunn et al. 2006). For amphibians, the temporary inundation of floodplain habitat is likely to influence distributions and abundances of species unevenly, reflecting variability in physiological, behavioral, and life-history characteristics of different species (Lytle 2001). De-

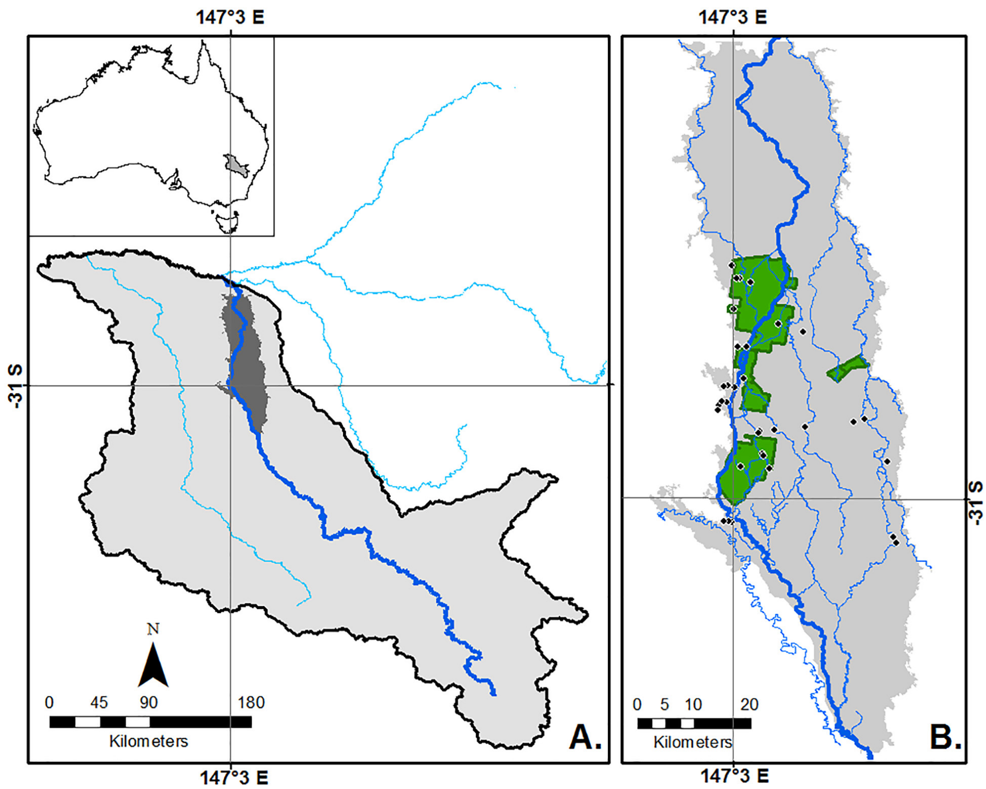


**Figure 1.** A. Location of Macquarie Marshes floodplain (dark grey shading) and the Macquarie River (dark blue) in the Macquarie-Bogan River catchment (light grey) in New South Wales, Australia. Location of catchment is shown in inset map. Light blue lines indicate major tributaries. B. Location of 30 survey sites (filled circles) on and adjacent to the Macquarie Marshes floodplain and creeks, and protected areas (green shading). Other features as in A.

termining which species are positively associated (i.e., higher abundance) with the habitat and conditions created by a flood pulse is an important step toward establishing ecologically relevant relationships between amphibian population status and floodplain inundation patterns. Much progress has been made towards this goal for some biotic groups (Arthur et al. 2012; Mims and Olden 2012), informing environmental management in degraded systems that target habitats or pre-regulation flow characteristics (e.g., timing, flood maximum) to benefit affected biota (Arthington 2012).

Our goals were to assess frog diversity in a large semi-arid floodplain wetland complex during a natural flood to evaluate how different species were influenced by floodplain inundation. We used unbiased estimates of relative abundance and detection probabilities to interpret abundance and distribution patterns as they related to physiological and behavioral features of different species. We hypothesized that species with similar features would have similar relationships with environmental variables. In particular, ground-dwelling species with low resistance to water-loss would be more abundant at permanently wet sites with predominantly low-lying aquatic vegetation, compared to arboreal species that would be more abundant in wooded areas and burrowing species that would be more abundant at non-floodplain grassland sites.

## Materials and Methods

We surveyed frog populations in the Macquarie Marshes (the Marshes), a Ramsar-listed large floodplain wetland (approximately 200,000 ha) in semi-arid Australia (Fig. 1). Flooding of the Marshes is highly dependent on rainfall in the upper parts of the catchment and resultant flows from the Macquarie River (Ren et al. 2010). Local annual rainfall varies considerably (mean = 449 ± [SD] 155 mm; range 126−1022 mm; years 1900−2014, Quambone Station; Bureau of Meteorology. 2016. Climate Data. Available from http://www.bom.gov.au/climate/data/ [Accessed 26 January 2016]). During the study period, widespread catchment rainfall, tributary flows and local rainfall over the Macquarie Marshes produced extensive flooding from early spring to late summer (September 2010 - March 2011).

We surveyed for frogs at 30 sites spread over 125,000 ha on and adjacent to the floodplain (Fig. 1). We stratified the 24 floodplain sites by dominant vegetation community, identified from existing vegetation mapping (Wilson 1992). Each community reflected a particular inundation frequency as measured by the average annual flooding return interval (ARI; Roberts and Marston 2000; Thomas et al. 2011). We included at least three sites within the five most widespread vegetation communities: Reed Bed (dominated by *Phragmites australis*) ARI = 0−1 y, $n$ = 3; Mixed Marsh (*Paspalum distichum* and *Ludwigia* spp.) ARI = 1−2 y, $n$ = 4; River Red Gum Woodland (*Eucalyptus camaldulensis*) ARI = 2−4 y, $n$ = 8; Black Box-Coolibah Woodland (*E. largiflorens*, *E. coolabah*) ARI = 6−8 y, $n$ = 5; and Chenopod Shrubland (*Salsola kali*, *Scleroleana muricata*) ARI = > 8 y, $n$ = 4. Six sites were located in Terrestrial Grassland (Umbrella Grass, *Chloris truncate*, and Warrego Summer Grass, *Paspalidium jubiflorum*) adjacent to the floodplain. We chose sites likely to be occupied by frogs: depressions naturally filled by rain ($n$ = 3) and farm dam ponds ($n$ = 3) permanently filled with water. All sites were separated by a minimum of 1 km. Survey sites were at least 50 m from other vegetation communities to minimize edge effects, except Reed Bed sites due to access difficulties.

We used a repeated measures sampling design for counts of each species from all 30 sites monthly from September 2010 to December 2010. High flood waters prevented access to one site in September and 10 sites in December. We randomized the order in which sites were surveyed each month, and surveyed sites close together on the same night to preclude the possibility of counting the same individual at multiple sites. During nocturnal site visits, we counted all frogs and identified them to species using visual and auditory encounter surveys (VAES) between 30 min after sunset (1900−2100) and 0300. At each site, we used two approaches: one 50 × 100 m area surveyed for one-person hour and three 50 × 4 m fixed transects using VAES. The first approach often surveyed areas adjacent to the transects but could be up to 100 m away from them due to varying water levels. We established these transects before the survey season but added the area surveys to increase coverage and flexibility at each site once surveys began due to increasing flood size. To reduce observer bias, surveys always included the first author and 2−3 experienced observers. To ensure reasonable accuracy of the count data, we walked the transect and area surveys slowly with two people next to each other to prevent double-counting, while another person walked behind recording their observations. We approached calling aggregations within the survey area very slowly to ensure each individual was located and identified. For each individual, we recorded the species, method of detection (seen only, heard only, or seen and heard), and life stage. If a vestigial tail stump was present, we recorded it as a metamorphosing individual but otherwise we recorded it as an adult. We could not accurately distinguish juveniles from adults for all species and so did not record them separately. Combining counts from both VAES methods for each species, we derived a total count of all adult individuals observed (seen and/or heard, excluding the recently metamorphosed individuals) and of all males recorded calling (heard only). Species taxonomy followed Frost (2015).

We used *N*-mixture models (Royle 2004) to estimate abundance, detection, and the influence of site- and survey-level covariates on abundance and detection of each species from our spatially and temporally replicated count data. Hierarchical models of abundance (*N*-mixture models) allow for comparisons of abundances of species at landscape scales while accounting for spatial and temporal variation in detection probabilities (Royle 2004). Census counts of amphibians rarely have perfect detection (Mazerolle et al. 2007), and not correcting for this issue produces erroneous estimates of abundance and distribution (Royle and Dorazio 2008) and bias in estimated relationships with ecological covariates (Gu and Swihart 2004). *N*-mixture models take the form of hierarchical generalized linear models, which can be solved through maximum likelihood estimation (MacKenzie et al. 2002). They have advantages over logistic or Poisson regression when modeling abundance because they allow for the estimation of abundance of the species as a function of site-level covariates, while accounting for imperfect species detection (Royle et al. 2007). By correcting for variable detection among sites and surveys, we reduced the bias in our abundance estimates to more accurately describe abundance across the landscape as it relates to environmental gradients. We modeled the variation in abundance distribution and detection probability with covariates using a logit-linear function.

We selected environmental variables to test for the influence of habitat and water permanency on abundances of species. We assessed habitat by assigning each site to one of three broad categories, determined by aggregating the dominant vegetation communities: Open-marsh Floodplain (Reed Bed, Mixed Marsh, and Chenopod Shrubland), Woodland-floodplain (River Red Gum Woodland and Black Box-Coolibah Woodland), and Terrestrial Grassland (natural depressions and farm dams). We aggregated water permanency categories to temporary (average return interval > 1 y or only filled with local rainfall) or permanently flooded (small dam ponds and Reed Bed sites) categories. These classifications improved model stability with few categories, while maintaining relevance to management plans.

We recorded two weather variables (temperature, rainfall) and two other survey-level variables (water depth, vegetation cover) at each site during each survey. We chose these variables as covariates for detection probability in our models due to their known or suspected influence on amphibian detection (Wassens et al. 2008; Canessa et al. 2012). We measured ambient air temperature using a Kestrel 3500 Weather Meter (Kestrel Weather, Birmingham, Mississippi, USA) at the start of each survey. We measured daily rainfall using a standard rain gauge near the center of the Macquarie Marshes (Fig. 1). We calculated daily (24 h) and weekly (7 d) rainfall (mm) but incorporated them into models as binary presence/absence states instead of continuous variables because there were few, highly variable rain events during all surveys, and this resulted in improved model performance. We recorded aquatic vegetation cover as the percentage cover of free-floating vegetation, floating and attached vegetation, submerged vegetation, short emergent vegetation (≤ 30 cm above water line), and tall emergent vegetation (> 30 cm above the water line) in three randomly positioned 5-$m^2$ quadrats within each site. We recorded water depth (cm) at the center of each quadrat. We tested for collinearity among predictor variables (temperature, daily rainfall, weekly rainfall, water depth, and aquatic vegetation cover) by determining if the variance inflation factor (VIF) of any variable had a value greater than five (O'Brien 2007). We standardized data (mean = 0, SD = 1) for all continuous variables (temperature, aquatic vegetation cover, and water depth) prior to analysis, providing stability for maximum likelihood estimates.

We modeled two response variables for each species: counts of all adults observed and counts of calling males. Abundance of all species was modeled as a zero-inflated Poisson distribution due to large numbers of zero counts, which resulted in overdispersed data (Joseph et al. 2009). We fit calling-only count models because calling males indicate potential suitable breeding habitat, which is crucial for assessing habitat use of a species during a flood. *N*-mixture models assumed the population was closed to mortality, recruitment, and migration. By confining our sampling to the relatively short but highly active four-month spring/early summer survey period, we considered that closure assumptions were reasonably met. No study species was known to have tadpoles that overwintered and may have recruited into the population during sampling, which we further ensured by not including recently metamorphosed frogs in the adult abundance counts. We only considered the portion of data for each species between the dates of first and last detection, as this ensured the species was available to be detected throughout that portion of the surveys, and also satisfied the closure assumption (MacKenzie et al. 2002).

We tested for spatial autocorrelation of each abundance of species between sites and survey periods using Moran's *I*. We adopted a conservative approach to reduce the chance of a false positive due to the multiple comparisons among species and included a spatially lagged response variable (SLRV; Threlfall et al. 2011) as an additional detection variable in the models (Haining 2003) if autocorrelation occurred in more than one survey period using a significance level of 0.01. The SLRV was calculated as weighted mean response for site, using the inverse distance as the weight and the $ln(x+1)$ transformation as the neighborhood values.

We used Akaike's information criterion, adjusted for small sample size (AICc; Burnham and Anderson 2002) to identify the best-supported model for both response variables (total adult and total calling) for each species. We first identified the best-supported model for detection probability with an intercept-only model for abundance. We compared all possible combinations of the four covariates (daily rain, weekly rain, average aquatic vegetation cover, water depth) but excluded models with both daily rainfall and weekly rainfall in the same model (24 combinations in total). We ranked models according to AICc. We used covariates from the best-supported model to calculate detection probabilities and to represent the detection process in subsequent model fitting.

To identify the best-supported model for the site-level abundance of each species (total adult and total calling), we compared all combinations of the site-level variables: habitat and water permanence. We ranked models again according to AICc, and assessed differences among species using the relationships and parameter estimates of the covariates from the best-supported model. If there was no clear top model (i.e., < 2 AICc points of the top model), then we used model averaging to calculate parameter estimates and confidence intervals. We assessed differences among the habitat categories (marsh, woodland, or grassland) by comparing the direction (positive or negative) and magnitude of the covariate coefficients, and if confidence intervals overlapped zero. We implemented the models in R 3.1.2 (R Core Team 2014) using the Unmarked (Fiske and Chandler 2011) and AICcmodavg (Mazerolle, M.J. 2012. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.25) packages.

## Results

We observed 15 species over 47 survey nights and 109 site surveys (average number of individuals per site survey = 39.9 ± [SE] 4.3; range 0–246). Ten nights had concurrent rain (range 2–28 mm). The December survey period had the highest rainfall total (99 mm), followed by November (88 mm), October (44 mm), and September (24 mm). All 15 species had been observed by the end of the third round of surveys (November 2010). The highest species richness occurred in the November and December surveys (14 species each;

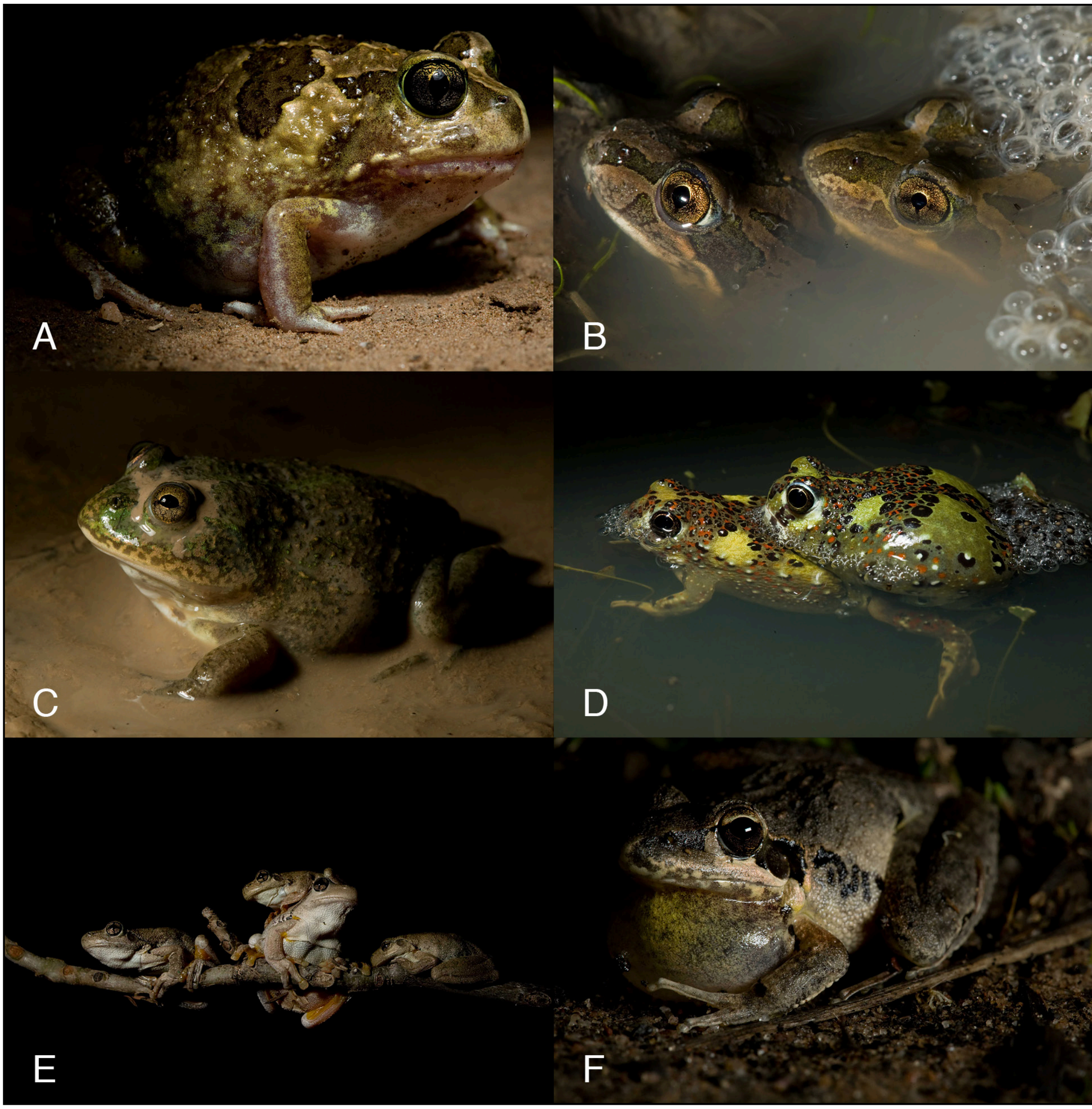


**Figure 2.** Six frogs of the Macquarie Marshes, New South Wales, Australia. A. Sudell's Burrowing Frog (*Neobatrachus sudelli*). B. Spotted Marsh Frog (*Limnodynastes tasmaniensis*). C. Water-holding Frog (*Litoria platycephala*). D. Crucifix Frog (*Notaden bennetti*). E. Peron's Tree Frog (*Litoria peroni*). F. Broad-palmed Rocket Frog (*Litoria latopalmata*). (All photographed by David Herasimtschuk).

the Warty Water-holding Frog, *Litoria verrucosa*, and Sudell's Frog, *Neobatrachus sudelli* [Fig. 2A], were the respective unobserved species).

Most observations of adults and of calling males were the Spotted Marsh Frog (*Limnodynastes tasmaniensis*; Fig. 2b), followed by the Barking Marsh Frog (*Limnodynastes fletcheri*) and the Eastern Sign-bearing Froglet (*Crinia parinsignifera*; Table 1). The fewest adults we observed were of the Water-holding Frog (*Litoria platycephala*; Fig. 2c) and Striped Burrowing Frog (*Litoria alboguttata*), whereas the fewest number of calling males we heard were the Ornate Burrowing Frog (*Playtplectrum ornatum*) and the Striped Burrowing Frog (Table 1).

The VIF values for all survey-level predictor variables were below five, so all were retained (Appendices 1 and 2). Our models successfully converged for 11 species using total adult observations, and for nine species using calling data (Tables 2, 3, and 4). Species with fewer than 15 observations (total adult or total calling, e.g., Water-holding Frog [$n$ = 4], Striped Burrowing Frog [$n$ = 2] or where most individuals were observed at one site on one occasion (e.g., 97% of Wrinkled Toadlet, *Uperoleia rugosa*, observations came from one site in

**Table 1.** The mean (± SE) and range (per site survey) of all adults and calling males of amphibian species observed in the Macquarie Marshes, Australia, during surveys of 30 sites, September to December 2010. † indicates a species where the model did not successfully converge using all adult counts; ‡ indicates where the model did not converge successfully using the calling counts.

| Family/Species | All adults | | Calling males only | |
|---|---|---|---|---|
| | Mean ± SE | Range | Mean ± SE | Range |
| Hylidae | | | | |
| Broad-palmed Rocket Frog (*Litoria latopalmata*) | 1.98 ± 0.39 | 0–21 | 1.52 ± 0.33 | 0–13 |
| Desert Tree Frog (*L. rubella*) | 0.89 ± 0.27 | 0–23 | 0.23 ± 0.08 | 0–5 |
| Green Tree Frog (*L. caerulea*) | 4.09 ± 1.22 | 0–83 | 0.74 ± 0.51 | 0–47 |
| Peron's Tree Frog (*L. peroni*) | 2.83 ± 0.67 | 0–45 | 2.31 ± 0.54 | 0–28 |
| Striped Burrowing Frog (*L. alboguttata*)†‡ | 0.02 ± 0.01 | 0–1 | 0.01 ± 0.01 | 0–1 |
| Warty Water-holding Frog (*L. verrucosa*)‡ | 0.17 ± 0.07 | 0–7 | 0.12 ± 0.08 | 0–7 |
| Water-holding Frog (*L. platycephala*)†‡ | 0.04 ± 0.02 | 0–1 | 0.04 ± 0.03 | 0–2 |
| Limnodynastidae | | | | |
| Barking Marsh Frog (*Limnodynastes fletcheri*) | 7.71 ± 1.10 | 0–60 | 6.81 ± 1.10 | 0–55 |
| Crucifix Frog (*Notaden bennetti*) | 0.28 ± 0.19 | 0–20 | 0.16 ± 0.14 | 0–13 |
| Ornate Burrowing Frog (*Playtplectrum ornatum*)†‡ | 0.05 ± 0.03 | 0–3 | 0.01 ± 0.01 | 0–1 |
| Salmon-striped Frog (*L. salmini*) | 0.93 ± 0.20 | 0–14 | 0.60 ± 0.20 | 0–14 |
| Spotted Marsh Frog (*L. tasmaniensis*) | 13.48 ± 2.84 | 0–241 | 14.99 ± 3.26 | 0–241 |
| Sudell's Frog (*Neobatrachus sudelli*)‡ | 0.09 ± 0.05 | 0–5 | 0.04 ± 0.03 | 0–2 |
| Myobatrachidae | | | | |
| Eastern Sign-bearing Froglet (*Crinia parinsignifera*) | 5.79 ± 1.88 | 0–141 | 6.78 ± 2.09 | 0–141 |
| Wrinkled Toadlet (*Uperoleia rugosa*)†‡ | 1.65 ± 1.60 | 0–174 | 1.81 ± 1.75 | 0–163 |

December) could not be adequately modeled. For these species, over half their total adult observations (58%) were during the 10 nights with rainfall. An SLRV was only included in the total adult abundance models for the Green Tree Frog (*Litoria caerulea*) as this was the only species in either data set (total adult or calling males) with spatial autocorrelation (three out of four survey periods; Appendices 3 and 4).

Detection probabilities varied among species and were influenced by covariates, although trends varied across species (Table 2). Greater air temperature (observed range, 9−28° C) generally increased detection probability, but detection of adults and calling males of two species decreased with increasing temperatures (Spotted Marsh Frog and Eastern Sign-bearing Frog) and two others were unaffected (Salmon-striped Frog, *Limnodynastes salmini*, and Sudell's Frog). Daily rainfall also had varying effects. It decreased the detection probability of the Spotted Marsh Frog, Salmon-striped Frog, and Eastern Sign-bearing Frog adults and calling males, but increased the probability of detecting Barking Marsh Frog, Crucifix Frog (*Notaden bennetti*; Fig. 2d), and Sudell's Frog, though confidence interval for Sudell's Frog included zero, indicating the relationship was not well supported. Daily rainfall or rain in the previous week were in the top detection models for total counts of adult Green Tree Frog, Desert Tree Frog (*Litoria rubella*), and Peron's Tree Frog (*Litoria peroni*; Fig. 2e), but confidence intervals for all estimates included zero (Table 2). By contrast, only weekly rainfall affected the probability of detection for the calling count models in these species, decreasing detection for the Green Tree Frog and increasing detection of Desert Tree Frog, Peron's Tree Frog, and the Broad-palmed Rocket Frog (*Litoria latopalmata*; Fig. 2f). Increased water depth and vegetation had varying effects, increasing detection of adults and calling males for some species and decreasing it for others (Table 2).

Adult and calling abundance differed among most species in relation to the habitat and water permanence variables (Tables 3 and 4, Appendix 5). Differences among categories (i.e., marsh floodplain, woodland-floodplain, and terrestrial grassland) occurred where 95% confidence intervals of covariate estimates did not include zero. For example, there was higher abundance of adult Spotted Marsh Frog in marsh compared to woodland and grassland sites (higher and positive parameter estimate with non-overlapping CIs; Table 3, Fig. 3, Appendix 5), and there was lower abundance in grassland compared to woodland sites (negative parameter estimate with non-overlapping CIs; Table 3). Adults and calling males of the Barking Marsh Frog, Striped

**Table 2.** Parameter estimates (95% CI) of detection (survey-specific) covariates for 11 (Abund.) and eight (Calling) frog species in the Macquarie Marshes, Australia. 'Response' (Resp.) refers to models using the total all adult count (Abund.) or the total calling males count (Calling) as the response variable. Differences occurred where 95% confidence intervals of covariate estimates did not include zero. W (weekly rainfall) and D (daily rainfall) indicate which rainfall variable was included in the model. An asterisk (*) indicates 95% CI of the variable did not overlap zero. Number of models (NM) in the best set based on AICc (models within 2 AICc points of the top ranked model).

| Family/Species | Resp. | NM | Intercept | Temperature | Rain | Water depth | Vegetation |
|---|---|---|---|---|---|---|---|
| Hylidae | | | | | | | |
| Broad-palmed Rocket Frog (*Litoria latopalmata*) | Abund. | 1 | -3 (-3.35, -2.7) | 0.8 (0.6, 1)* | — | — | -0.2 (-0.4, -0.005) |
| | Calling | 3 | -4 (-4.8, -3.7) | 0.7 (0.4, 0.9)* | 0.7 (0.2, 1.1) (W)* | — | — |
| Desert Tree Frog (*L. rubella*) | Abund. | 2 | -4 (-4.6, -3.5) | 0.5 (0.2, 0.7)* | 0.4 (-0.01, 0.8) (W) | — | — |
| | Calling | 1 | -5 (-6.4, -3.8) | 1 (0.4, 1.7)* | 0.2 (-0.1, 0.6) (D) | — | — |
| Green Tree Frog (*L. caerulea*)† | Abund. | 1 | -3 (-3.6, -2.9) | 1.2 (1.1, 1.3)* | -0.3 (-0.5, 0.2) (D) | — | -0.2 (-0.5, 0.0) |
| | Calling | 3 | -7 (-8.3, -5.7) | 3.6 (2.5, 4.8)* | 1.5 (0.7, 2.3) (W)* | 1 (0.35, 1.5)* | -1 (-1.9, -0.03)* |
| Peron's Tree Frog (*L. peroni*) | Abund. | 1 | -2.4 (-3.3, -1.5) | 0.5 (0.2, 0.6)* | -0.1 (-0.3, 0.06) (D) | -0.6 (-0.8, -0.4)* | — |
| | Calling | 1 | -2.7 (-3.4, -2) | 0.5 (0.3, 0.7)* | 0.4 (0.16, 0.6) (W)* | -0.4 (-0.7, -0.2)* | — |
| Warty Water-holding Frog (*L. verrucosa*) | Abund. | 1 | -6.9 (-9.2, -4.6) | 2.3 (1.3, 3.3)* | — | — | — |
| Limnodynastidae | | | | | | | |
| Barking Marsh Frog (*Limnodynastes fletcheri*) | Abund. | 1 | -1.9 (-2.3, -1.5) | 0.6 (0.5, 0.7)* | — | — | 0.4 (0.2, 0.5)* |
| | Calling | 1 | -2.5 (-2.7, -2.3) | 0.4 (0.3, 0.5)* | 0.2 (0.1, 0.2) (D)* | 0.1 (-0.03, 0.24) | 0.4 (0.3, 0.5)* |
| Crucifix Frog (*Notaden bennetti*) | Abund. | 2 | -8 (-10, -6) | 2.2 (1, 3.2)* | 0.8 (0.4, 1.2) (D)* | -2.6 (-4.1, -1.1)* | 0.9 (0, 1.7) |
| Salmon-striped Frog (*L. salmini*) | Abund. | 3 | -2.9 (-5, -0.8) | — | -0.5 (-0.9,-0.2) (D)* | — | — |
| | Calling | 1 | -3.3 (-4.9, -1.8) | — | -0.5 (-0.9,-0.3) (D)* | — | -0.3 (-0.7, 0.01) |
| Spotted Marsh Frog (*L. tasmaniensis*) | Abund. | 1 | -2.2 (-2.3,-2.02) | -0.7 (-0.78, -0.67)* | -0.3 (-0.4,-0.2) (D)* | -0.03 (-0.1, 0.07) | — |
| | Calling | 1 | -1.9 (-2, -1.7) | -0.6 (-0.7, -0.55)* | -0.4 (-0.5,-0.3) (D)* | — | -0.4 (-0.5, -0.3*) |
| Sudell's Frog (*Neobatrachus sudelli*) | Abund. | 4 | -3 (-6.3, 0.3) | — | 0.5 (-0.2, 1.2) (D) | — | — |
| Myobatrachidae | | | | | | | |
| Eastern Sign-bearing Frog (*Crinia parinsignifera*) | Abund. | 1 | -2.3 (-2.4, -2.1) | -0.4 (-0.5, -0.35)* | -0.4 (-0.5,-0.3) (D)* | -0.1 (-0.3,-0.02)* | — |
| | Calling | 1 | -2.2 (-2.3, -2.1) | -0.45 (-0.5, -0.35)* | -0.3 (-0.4,-0.2) (D)* | -0.1 (-0.3,-0.01)* | — |

† Spatial lagged response variable (SLVR) was included as a covariate

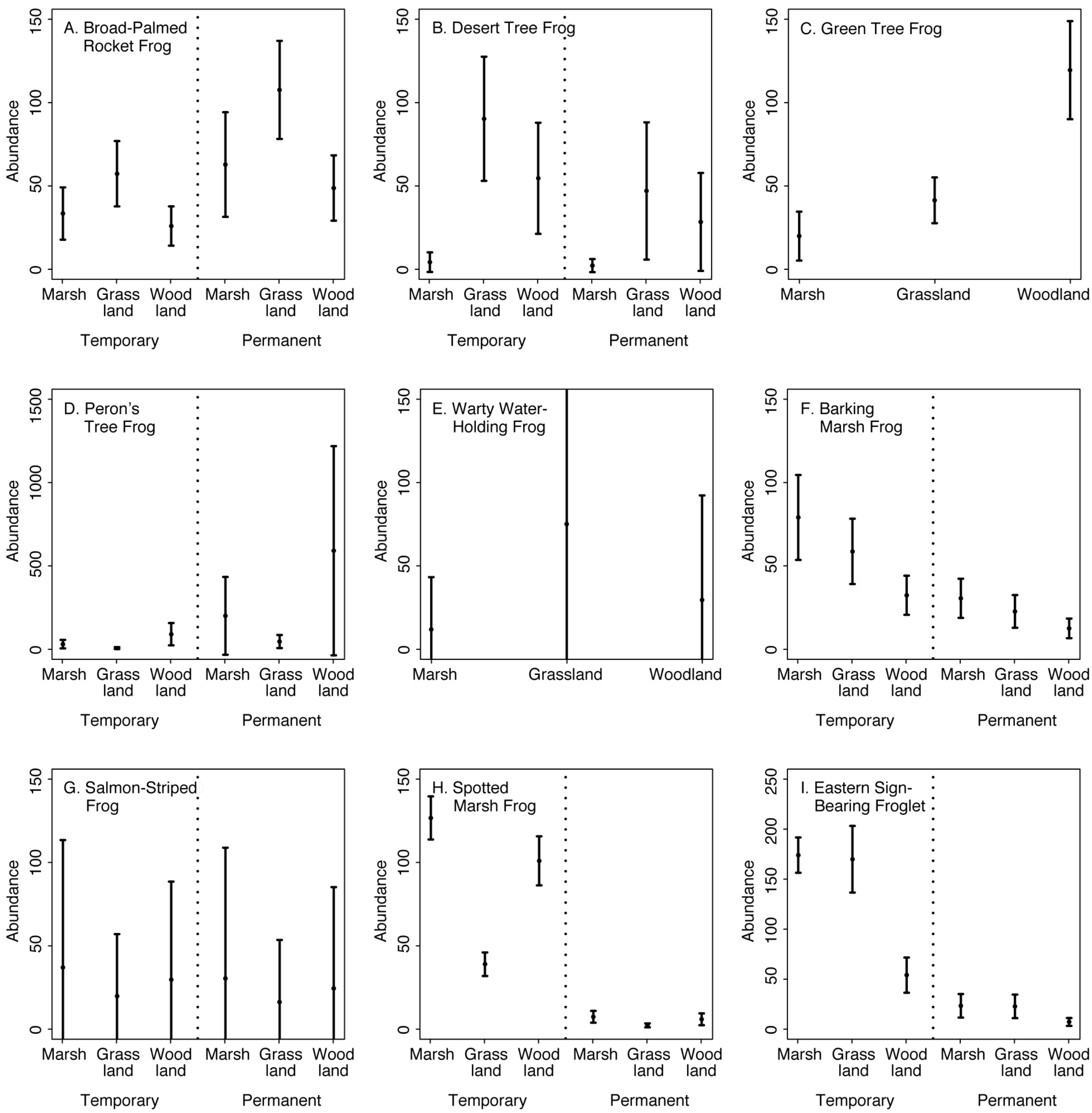


**FIGURE 3.** Mean (± 95% CI) abundance estimates (i.e., number of individuals) of adult frogs for the landscape-scale site variables (habitat and water-type [Temporary or Permanent]) derived from the best-ranked model for nine frog species in the Macquarie Marshes, New South Wales, Australia, during a large natural flood. A. Broad-palmed Rocket Frog (*Litoria latopalmata*). B. Desert Tree Frog (*Litoria rubella*). C. Green Tree Frog (*Litoria caerulea*). D. Peron's Tree Frog (*Litoria peroni*). E. Warty Water-holding Frog (*Litoria verrucosa*). F. Barking Marsh Frog (*Limnodynastes fletcheri*). G. Salmon-striped Frog (*Limnodynastes salmini*). H. Spotted Marsh Frog (*Limnodynastes tasmaniensis*). I. Eastern Sign-bearing Froglet (*Crinia parinsignifera*). Crucifix Frog (*Notaden bennetti*) and Sudell's Burrowing Frog (*Neobatrachus sudelli*) are not shown as no landscape-scale variables had a clear influence on abundance. Plots with both landscape-scale variables show abundance for all combinations of habitat and water-type (i.e., Broad-palmed Rocket Frog).

Marsh Frog, and Eastern Sign-bearing Froglet were more abundant at marsh and temporarily flooded sites than other sites (Tables 3 and 4, Fig. 3). The abundance of adult and calling Salmon-striped Frogs was also positively influenced by marsh sites though estimates included zero, and water permanence was not included in the top model set. Broad-palmed Rocket Frog adults were more abundant at permanently wet grassland sites, but this changed to no influence of water permanence for calling males. Adult and calling Peron's Tree Frog were more abundant at permanently wet woodland sites than marsh or grassland sites (Fig. 3). Green Tree Frog

**Table 3.** Parameter estimates (95% CI) of landscape (site-specific) covariates for 11 (Abund.) and eight (Calling) frog species in the Macquarie Marshes, Australia. 'Response' (Resp.) refers to models using the total all adult count (Abund.) or the total calling males count (Calling) as the response variable. We obtained parameter estimates by comparing categories against the dummy variable in the model (Woodland for habitat type and Permanent for water type, represented by 'vs'). An asterisk (*) indicates 95% CI of the variable that did not overlap zero. A positive parameter estimate with 95% CI not overlapping zero indicated that habitat type had a clear positive influence on abundance. Number of models (NM) in the best set based on AICc (models within 2 AICc points of the top ranked model).

| Species | Resp. | NM | Intercept | Marsh vs. Woodland | Grassland vs. Woodland | Permanent vs. temporary |
|---|---|---|---|---|---|---|
| Hylidae | | | | | | |
| Broad-palmed Rocket Frog (*Litoria latopalmata*) | Abund. | 1 | 3.3 (2.8, 3.7) | 0.2 (-0.2, 0.7) | 0.8 (0.4, 1.1)* | 0.6 (0.3, 1)* |
| | Calling | 3 | 4 (3.5, 4.7) | 0.24 (-0.3, 0.76) | 0.5 (0.1, 0.9)* | -0.8 (-1.9, 0.3) |
| Desert Tree Frog (*L. rubella*) | Abund. | 2 | 4 (3.4, 4.7) | -2.6 (-4.2, -1)* | 0.45 (-0.04, 1) | -0.65 (-1.4, 0.1) |
| | Calling | 1 | 2.9 (1.3, 4.5) | -0.3 (-2.1, 1.5) | 1.4 (0.2, 2.6)* | — |
| Green Tree Frog (*L. caerulea*) | Abund. | 1 | 3.2 (2.8, 3.5) | -0.9 (-1.5, -0.1)* | 1.4 (1.1, 1.7)* | — |
| | Calling | 2 | 4.7 (4.5, 5) | -12 (-465, 440) | -1.2, (-2, -0.5)* | -12 (-705, 680) |
| Peron's tree frog (*L. peroni*) | Abund. | 1 | 4.5 (3.8, 5.2) | -1.1 (-1.6, -0.5)* | -2.5 (-3, -2)* | 1.5 (0.4, 2.5)* |
| | Calling | 1 | 4.4 (3.8, 5) | -0.7 (-1.3, -0.11)* | -2.5 (-3.1, -1.9)* | — |
| Warty Water-holding Frog (*L. verrucosa*) | Abund. | 1 | 4.3 (3.2, 5.5) | — | — | — |
| Limnodynastidae | | | | | | |
| Barking Marsh Frog (*Limnodynastes fletcheri*) | Abund. | 1 | 3.5 (3.1, 3.8) | 0.9 (0.6, 1.1)* | 0.6 (0.4, 0.8)* | -1 (-0.2, -0.7)* |
| | Calling | 1 | 3.9 (3.6, 4.2) | 0.9 (0.6, 1.1)* | 0.3 (0.02,0.6)* | -1.2 (-1.5, -0.8)* |
| Crucifix Frog (*Notaden bennetti*) | Abund. | 4 | 2 (-0.1, 4) | -10, (-235, 214) | 1 (-1.8, 3.8) | -10 (-236, 214) |
| Salmon-striped Frog (*L. salmini*) | Abund. | 3 | 3.3 (1.2, 5.3) | 0.2 (-0.3, 0.7) | -0.5 (-1, 0.03) | -0.8 (-1.8, 0.3) |
| | Calling | 1 | 4 (3.2, 4.8) | 0.4 (-0.1, 1) | -1.3 (-2.3, -0.3)* | -13 (-398, 371) |
| Spotted Marsh Frog (*L. tasmaniensis*) | Abund. | 1 | 5.1 (5, 5.3) | 0.2 (0.1, 0.36)* | -1 (-1.1, -0.8)* | -2.8 (-3.4, -2.3)* |
| | Calling | 1 | 4.8 (4.7, 5) | 0.4 (0.3, 0.60)* | -0.8 (-0.9, -0.6)* | -2.8 (-3.9, -1.7)* |
| Sudell's Frog (*Neobatrachus sudelli*) | Abund. | 4 | -1 (-68, 66) | -7 (-496, 483) | 9.6 (-109, 128) | -12 (-629, 604) |
| Myobatrachidae | | | | | | |
| Eastern Sign-bearing Frog (*Crinia parinsignifera*) | Abund. | 1 | 4 (3.7, 4.3) | 1.2 (0.8, 1.5)* | 1.1 (0.8, 1.5)* | -2 (-2.5, -1.5)* |
| | Calling | 1 | 4 (3.7, 4.3) | 1.2 (0.8, 1.5)* | 1.2 (0.9, 1.5)* | -1.9 (-2.5, -1.4)* |

and Desert Tree Frog abundance had more complex associations with habitat that changed between adult and calling males, though marsh sites consistently had the smallest influence (Table 1). Neither species were influenced by water permanency. However, the SLRV term had a positive relationship (0.2, CI = 0.1, 0.3) with Green Tree Frog abundance, indicating this species was more likely to be in one area if there were large numbers nearby. The best models for the Warty Water-holding Frog, Sudell's Burrowing Frog, and Crucifix Frog included parameter estimates for habitat and water permanency, but all estimates included zero, indicating little evidence for influence of any variable (Table 3).

## Discussion

Conservation data for managing large floodplains around the world remain poor even in reasonably well-studied river systems such as those in Australia. This was one of the few systematic surveys of frog populations in

**Table 4.** Summary of relative importance of variables showing the influence of landscape (site-specific) covariates on abundance and survey-specific covariates on detection of all adults of 11 frog species (Abund.) and only calling males of nine frog species (Calling) in the Macquarie Marshes, Australia, based on Tables 2 and 3, and Appendix 5. Only covariates with 95% confidence intervals not including zero are shown. The order of the landscape habitat variables was determined from the model results in Table 3 and Appendix 5. Habitat variables on the left of '>' had a positive and higher parameter estimate than the habitat on the right. '=' indicates there was no difference between the two habitats (95% CI overlapped zero). 'Water type' indicates the category that had a positive influence on abundance when compared to the other category in the models. '+' and '-' indicate if the survey variable had a positive or negative influence detection. W (weekly rainfall) and D (daily rainfall) indicate which rainfall variable was included in the model.

| | | Landscape variables (abundance) | | Survey variables (detection) | | | |
|---|---|---|---|---|---|---|---|
| Species | Resp. | Habitat | Water type | Temperature | Rain | Water depth | Vegetation |
| Hylidae | | | | | | | |
| Broad-palmed Rocket Frog (*Litoria latopalmata*) | Abund. | grassland > marsh = woodland | permanent | + | | | |
| | Calling | grassland > woodland grassland = marsh, woodland = marsh | | + | + (W) | | |
| Desert Tree Frog (*L. rubella*) | Abund. | grassland = woodland > marsh | | + | | | |
| | Calling | grassland > woodland = marsh | | + | | | |
| Green Tree Frog (*L. caerulea*) | Abund. | woodland > grassland = marsh | | + | | | |
| | Calling | woodland > grassland grassland = marsh, woodland = marsh | | + | + (W) | + | - |
| Peron's tree frog (*L. peroni*) | Abund. | woodland > marsh > grassland | permanent | + | | - | |
| | Calling | woodland > marsh > grassland | permanent | + | + (W) | - | |
| Warty Water-holding Frog (*L. verrucosa*) | Abund. | | | + | | | |
| Limnodynastidae | | | | | | | |
| Barking Marsh Frog (*Limnodynastes fletcheri*) | Abund. | marsh > grassland > woodland | temporary | + | | | + |
| | Calling | marsh > grassland > woodland | temporary | + | + (D) | | + |
| Crucifix Frog (*Notaden bennetti*) | Abund. | | | | + (D) | | |
| Salmon-striped Frog (*Limnodynastes salmini*) | Abund. | marsh = woodland = grassland | | | - (D) | | |
| | Calling | marsh = woodland > grassland | | | - (D) | | |
| Spotted Marsh Frog (*L. tasmaniensis*) | Abund. | marsh > woodland > grassland | temporary | - | - (D) | | |
| | Calling | marsh > woodland > grassland | temporary | - | - (D) | | - |
| Sudell's Frog (*Neobatrachus sudelli*) | Abund. | | | | | | |
| Myobatrachidae | | | | | | | |
| Eastern Sign-bearing Frog (*Crinia parinsignifera*) | Abund. | marsh = grassland > woodland | temporary | - | - (D) | - | |
| | Calling | marsh = grassland > woodland | temporary | - | - (D) | - | |

large semi-arid wetland complexes in inland Australia and the first in the Ramsar-listed Macquarie Marshes. We detected 14 species recorded in earlier sporadic surveys in the Marshes and one further species that had not been previously observed (Ornate Burrowing Frog; Brooker and Wombey 1986; Shelley 2005). The overall flood extent was the largest experienced in the Marshes for 10 y (Thomas et al. 2015) and coincided with some of the highest monthly local rainfall totals also seen in recent years (December 2010, 99 mm; mean of previous 10 y [2000−2009] = 40 ± [SD] 46 mm; range 0−270 mm). There were highly variable influences of floodplain habitat and water permanency on frog abundance, and survey-level variables (i.e., rain, temperature) on frog detection. However, there were general similarities in abundance patterns of different species of frogs with similar physiological and behavioral features, which are relevant for conservation management. These patterns highlighted the species that were likely to have a positive association with actively managed floods aimed at benefitting wetland biota by maintaining wetting-drying patterns across the floodplain.

The Spotted Marsh Frog, Barking Marsh Frog, and Eastern Sign-bearing Froglet had the highest average abundance and showed similar relationships with habitat and water permanency. Detection-corrected abundance of both adults and calling males was consistently highest in some flooded areas, typically temporary wetlands with low-lying aquatic vegetation. Temporarily flooded areas probably provided suitable breeding and shelter habitat due to lagged colonization by tadpole predators such as fish and odonates and foraging potential due to high levels of primary production and prey items such as invertebrates (Boulton et al. 2006). Aquatic vegetation cover within a wetland also provides shelter from predators, attachment sites for egg clutches, and substrate for tadpole food sources such as algal biofilm (Altig et al. 2007). These three species have long tadpole development (> 3 mo; Anstis 2013) and lack specialized physiological traits, such as cocoon-building or high resistance to evaporative water loss (Lee and Mercer 1967; Young et al. 2005) that would allow survival in dry conditions. Inundation duration from river flows may often be longer than for rain-filled temporary sites, especially in dryland areas with high evaporation rates, and floodplain habitats are therefore important for providing sufficiently long hydroperiod for tadpoles that require several months to complete metamorphosis.

Other frog species in the Marshes that shared similar physiological and behavioral traits also showed broadly similar responses to environmental factors. The Green Tree Frog, Desert Tree Frog, and Peron's Tree Frog are arboreal-adapted hylid species with specialized toe-discs for climbing and a relatively high resistance to water-loss, which likely allows sheltering in relatively dry environments (Young et al. 2005; Tracy et al. 2010). During the flood, these species were typically more abundant in woodland habitat but generally unaffected by the duration of water at sites. Both Green Tree Frogs and Desert Tree Frogs are widely distributed across northern Australia, where their breeding is mostly associated with rainfall (Anstis 2013). These species successfully exploit water bodies with brief hydroperiods due to their short period of tadpole development. This species and others with ecological similarities (e.g., *Hyla chrysoscelis*; Eskew et al. 2012) are probably less dependent on flooded habitats and resources for shelter and breeding. The spatial autocorrelation detected in abundance of Green Tree Frogs made interpretation of abundance patterns difficult. Several interpretations were possible, including a potential metapopulation structure as a result of habitat patchiness (Hanski 1998), or autocorrelation in unmeasured variables leading to apparent clusters in abundance regardless of habitat patchiness. There was little evidence for a metapopulation structure in the other species (e.g., limited spatial autocorrelation in abundances), possibly reflecting the continuous nature of floodplain habitat compared to discrete ponds (Haining 2003).

Floodplain habitat and conditions during the flood had little influence on abundances of Salmon-striped Frog, Striped Burrowing Frog, Sudell's Frog, and Crucifix Frog. These species were burrowing frogs that spend most of their time underground either encased in a cocoon or moving with the water table (Withers 1995; Booth 2006; Cartledge et al. 2006). They emerge, often using specialized hardened spades (metatarsal tubercles), with explosive populations following rainfall, particularly in warmer months (Read 1999). It was not surprising that we could not successfully model abundances of these species since they occurred in very low numbers at a limited number of sites or in large numbers only after substantial rainfall, similar to the other species burrowing species we were unable to model such as the Wrinkled Toadlet and Warty Water-holding Frog. High rainfall was likely the primary driver of detection, and abundance was not affected by any habitat characteristics that we measured. Although they called in flooded habitat, it was only during substantial local rainfall (> 100 mm rain over five nights, 29 November to 3 December 2010). It would be useful to investigate the responses of these frogs in an area not affected by flooding but only rainfall and to identify other potential habitat characteristics (e.g., prey abundance) or soil type influencing abundance (Dayton et al. 2004).

Weather influenced detection of frogs, though with considerable variation among the species as previous studies have indicated (MacKenzie et al. 2002; Canessa et al. 2012). While temperature and rainfall are often identified as having a strong influence on activity and detection (Chan-McLeod 2003; Pellet and Schmidt 2005), the strength of each may vary spatially within the range of a species across altitudes and bioclimatic regions (Navas 1996; Dostine et al. 2013), though there are few data from outside of temperate regions (Ocock et al. 2014). During our study, temperature and rainfall may not have been as strong because of the widespread availability of water due to flooding. This reinforces the importance of surveying for frogs on multiple occasions over varying climatic conditions in wetlands of semi-arid regions.

The Broad-palmed Rocket Frog was the only species to show a clear change in habitat between response types. While general adult abundance was higher at permanent water sites, calling males showed no influence of water type. This suggests there is little distinction between the diverse habitat types used for breeding and for general activity in most species on floodplain wetlands, unlike other areas where species may move between breeding and non-breeding habitats (Semlitsch and Bodie 2003). Inundation and water availability probably primarily dictate suitability of habitat for breeding activity.

Conservation of ecosystems such as the Macquarie Marshes is highly dependent on protection of river flows from water resource developments. Water diversion and regulation affects most large rivers of the world (Nilsson et al. 2005), considerably changing flow regimes and reducing inundation of aquatic ecosystems. These alterations impact amphibian communities (Wassens and Maher 2011; Eskew et al. 2012), water bird communities (Kingsford and Thomas 1995), and flood-dependent vegetation health and distribution (Stromberg et al. 2012). Though our current understanding of amphibian ecology in floodplain wetland systems is reasonably poor compared to other biota (Kingsford 2006), it is likely that frequent, albeit variable, inundation creates suitable conditions for higher amphibian species diversity than would otherwise occur in arid and semi-arid regions (Slatyer et al. 2007) and drives changes in population size and distribution of some species (Tockner et al. 2006; McGinness et al. 2014). Our surveys suggest that despite low rainfall and a high evaporation rate, the Marshes provide substantial habitat for species that have few specialized adaptations to water loss. This includes the Barking Marsh Frog and Spotted Marsh Frog, which have almost no cutaneous resistance to water loss (Amey and Grigg 1995), compared to arboreal and burrowing species that have partly escaped dependence on water (Tracy et al. 2010; Anstis 2013). The occurrence during our study of all species known from the Marshes indicated a degree of resilience through the decade-long drought. Species with high abundance during a flood, like the Barking Marsh Frog and the Spotted Marsh Frog, are unlikely to become extinct across their range due to effects of regulation, as breeding and recruitment also occur during flooding caused by local rainfall. However, if future management actions do not favor the wetland environment, the cumulative effect of smaller and less frequent floods will equate with lower overall frog abundance of species positively influenced by temporary inundation of floodplain wetlands. This may limit dispersal and isolate populations (Wassens et al. 2008), as well as have implications for wetland foodwebs and overall productivity (Kingsford 2000). Managing flows in regulated systems to mimic natural flooding patterns is likely crucial for maintaining their distribution and populations. Comparisons of frog responses during high local rainfall and low flood years would be particularly interesting in separating out the confounding effects of rainfall and flooding and identifying the true dependencies of various species. This would further inform flow management strategies that could benefit frog populations as well as other biota.

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**Appendix 1.** Results of covariance matrix among the survey level predictor variables.

| | Daily rainfall | Air temperature | Water depth | Aquatic vegetation cover | Weekly rainfall |
|---|---|---|---|---|---|
| Daily rainfall | 26.79 | 1.28 | -4.88 | -31.23 | 44.43 |
| Air temperature | 1.28 | 18.59 | -4.96 | 68.12 | 59.09 |
| Water depth | -4.88 | -4.96 | 154.52 | 91.18 | -1.05 |
| Aquatic vegetation cover | -31.23 | 68.12 | 91.18 | 1725.43 | 22.34 |
| Weekly rainfall | 44.43 | 59.09 | -1.05 | 22.34 | 709.67 |

**Appendix 2.** The variance inflation factor (VIF) for the survey level predictor variables. Values higher than five indicate collinearity.

| Variable | VIF |
|---|---|
| Daily rainfall | 1.157 |
| Air temperature | 1.758 |
| Water depth | 1.083 |
| Aquatic vegetation cover | 1.322 |
| Weekly rainfall | 1.612 |

**Appendix 3.** Results of test for spatial autocorrelation of the total adult abundance response variable using Moran's *I* among survey months for each species. Alpha significance was set at 0.01 to cautiously reduce the chance of a false positive due to the multiple comparisons. Missing values indicate that species was not detected during that survey period.

| Family/Species | Survey month | | | |
|---|---|---|---|---|
| | Sept. | Oct. | Nov. | Dec. |
| Hylidae | | | | |
| Striped Burrowing Frog (*Litoria alboguttata*) | 0.27 | 0.27 | — | — |
| Green Tree Frog (*Litoria caerulea*) | < 0.01 | < 0.01 | < 0.01 | < 0.01 |
| Broad-palmed Rocket Frog (*Litoria latopalmata*) | 0.87 | 0.87 | 0.04 | 0.86 |
| Peron's Tree Frog (*Litoria peroni*) | 0.04 | 0.04 | < 0.01 | 0.27 |
| Water-holding Frog (*Litoria platycephala*) | — | — | 0.18 | 0.33 |
| Desert Tree Frog (*Litoria rubella*) | 0.54 | 0.54 | 0.37 | 0.05 |
| Warty Water-holding Frog (*Litoria verrucosa*) | 0.27 | 0.27 | — | 0.78 |
| Limnodynastidae | | | | |
| Barking Marsh Frog (*Limnodynastes fletcheri*) | 0.06 | 0.06 | 0.96 | 0.06 |
| Salmon-striped Frog (*Limnodynastes salmini*) | 0.01 | 0.01 | 0.81 | 0.95 |
| Spotted Marsh Frog (*Limnodynastes tasmaniensis*) | 0.38 | 0.38 | 0.15 | 0.45 |
| Sudell's Frog (*Neobatrachus sudelli*) | 0.79 | 0.79 | 0.76 | 0.18 |
| Crucifix Frog (*Notaden bennetti*) | — | — | 0.76 | 0.71 |
| Ornate Burrowing Frog (*Playtplectrum ornatum*) | — | — | 0.40 | 0.37 |
| Myobatrachidae | | | | |
| Eastern Sign-bearing Froglet (*Crinia parinsignifera*) | 0.06 | 0.06 | < 0.01 | 0.43 |
| Wrinkled Toadlet (*Uperoleia rugosa*) | — | — | 0.25 | 0.81 |

**Appendix 4.** Results of test for spatial autocorrelation of the calling males abundance response variable using Moran's *I* among survey months for each species. Alpha significance was set at 0.01 to cautiously reduce the chance of a false positive due to the multiple comparisons. Missing values indicate that species was not detected during that survey period.

| Species | Survey month | | | |
|---|---|---|---|---|
| | Sept | Oct | Nov | Dec |
| Hylidae | | | | |
| Striped Burrowing Frog (*Litoria alboguttata*) | — | — | — | 0.80 |
| Green Tree Frog (*Litoria caerulea*) | 0.39 | — | 0.86 | < 0.01 |
| Broad-palmed Rocket Frog (*Litoria latopalmata*) | | 0.41 | 0.29 | 0.94 |
| Peron's Tree Frog (*Litoria peroni*) | 0.09 | < 0.01 | 0.13 | 0.73 |
| Water-holding Frog (*Litoria platycephala*) | — | — | 0.17 | 0.33 |
| Desert Tree Frog (*Litoria rubella*) | — | 0.31 | 0.15 | 0.86 |
| Warty Water-holding Frog (*Litoria verrucosa*) | — | — | 0.17 | 0.37 |
| Limnodynastidae | | | | |
| Barking Marsh Frog (*Limnodynastes fletcheri*) | 0.78 | 0.90 | 0.03 | 0.96 |
| Salmon-striped Frog (*Limnodynastes salmini*) | 0.02 | 0.21 | 0.45 | < 0.01 |
| Spotted Marsh Frog (*Limnodynastes tasmaniensis*) | 0.07 | 0.78 | 0.66 | 0.51 |
| Sudell's Frog (*Neobatrachus sudelli*) | 0.31 | — | 0.17 | — |
| Crucifix Frog (*Notaden bennetti*) | | — | 0.17 | 0.36 |
| Ornate Burrowing Frog (*Playtplectrum ornatum*) | — | — | — | 0.62 |
| Myobatrachidae | | | | |
| Eastern Sign-bearing Froglet (*Crinia parinsignifera*) | 0.14 | < 0.01 | 0.57 | 0.96 |
| Wrinkled Toadlet (*Uperoleia rugosa*) | — | — | 0.29 | 0.80 |

**Appendix 5.** Parameter estimates (95% CI) of the marsh habitat category compared to grassland for 11 (Abund.) and eight (Calling) frog species in the Macquarie Marshes. 'Response' refers to models using the total all adult count (Abund.) or the total calling males count (Calling) as the response variable. * indicates 95% CI of the variable did not overlap zero.

| Species | Response | No. of models[a] | Intercept | Marsh vs. Grassland |
|---|---|---|---|---|
| Hylidae | | | | |
| Broad-palmed Rocket Frog (*Litoria latopalmata*) | Abund. | 1 | 4 (3.7, 4.4) | -0.5(-0.9, -0.1)* |
| | Calling | 4 | 4.5 (4.2, 4.8) | -0.3 (-0.8, -0.2)* |
| Desert Tree Frog (*Litoria rubella*) | Abund. | 2 | 4.5 (4.1, 4.9) | -3 (-4.5, -1.5)* |
| | Calling | 2 | 4.3 (3.3, 5.4) | -1.7, (-3.4, -0.1)* |
| Green Tree Frog (*Litoria caerulea*) | Abund. | 1 | 3.5 (3.1, 3.9) | -0.4 (-1.0, 0.3) |
| | Calling | 4 | 4.5 (3.7, 5.4) | -12 (-563, 539) |
| Peron's tree frog (*Litoria peroni*) | Abund. | 1 | 2 (1.1, 2.8) | 1.5 (0.7, 2.2)* |
| | Calling | 1 | 1.9 (1.1, 2.7) | 1.8 (1, 2.7)* |
| Warty Water-holding Frog (*Litoria verrucosa*) | Abund. | | | |
| Limnodynastidae | | | | |
| Barking Marsh Frog (*Limnodynastes fletcheri*) | Abund. | 1 | 4 (3.7, 4.4) | 0.3 (0.1, 0.5)* |
| | Calling | 1 | 4.2 (3.9, 4.4) | 0.5 (0.3, 0.8)* |
| Crucifix Frog (*Notaden bennetti*) | Abund. | 1 | | |
| Salmon-striped Frog (*Limnodynastes salmini*) | Abund. | 3 | 3.6 (1.7, 5) | 0.6 (0.0, 1.1) |
| | Calling | 1 | 2.7 (4.6, 3.8) | 1.7 (0.8, 2.7)* |
| Spotted Marsh Frog (*Limnodynastes tasmaniensis*) | Abund. | 1 | 4.2 (4, 4.3) | 1.2 (1, 1.4)* |
| | Calling | 1 | 4.3 (4.1, 4.5) | 1 (0.9, 1.2)* |
| Sudell's Frog (*Neobatrachus sudelli*) | Abund. | 4 | 2.2 (-1, 5.3) | -10 (-251, 229) |
| Myobatrachidae | | | | |
| Eastern Sign-bearing Frog (*Crinia parinsignifera*) | Abund. | 1 | 5 (4.9, 5.3) | 0.02 (-0.2, 0.2) |
| | Calling | 1 | 5.2 (5, 5.4) | -0.04 (-0.2, 0.2) |

[a] Number of models in the best set based on AICc (models within 2 AICc points of the top ranked model).