

Determining environmental limits of threatened species: the example of the wallum sedgefrog *Litoria olongburensis*

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Abstract. In an environment that is changing due to anthropogenic processes, managers responsible for conservation of threatened species need to know environmental limits beyond which those species are at risk of extinction. We demonstrate estimation of environmental limits for a threatened species using a novel combination of response modeling techniques. Our study species was *Litoria olongburensis* (wallum sedgefrog), which has a biphasic lifecycle (aquatic larvae and terrestrial adult phases) with larvae developing in naturally acidic wetlands of coastal sandy lowlands (“wallum”) of subtropical eastern Australia. Land development in, and around, areas occupied by the frog is the main cause of the species’ decline, while climate change is emerging as a new threat. The species will continue to decline where these processes destroy, fragment or degrade habitat. We surveyed waterbodies throughout the latitudinal range of the species’ distribution, recording wallum sedgefrog density and environmental variables including abiotic waterbody characteristics, key vegetation types, potential competitors and potential predators. For each environmental variable, we tested the fit of increasingly complex response models to the highest possible quantile of wallum sedgefrog density. The best-fitting model indicated the most likely response, if any, to the variable. This model was then applied to estimate environmental limits. Our analysis indicated wallum sedgefrogs were less likely to occur in waterbodies with pH outside 3.53–4.61 (± 0.11) and maximum water depth outside 23.4–46.0 (± 3.5) cm, and their density decreased with increasing densities of eastern sedgefrogs, wallum froglets and common froglets. The optimal pH levels and water depths indicated by our analysis provide a necessary baseline for predicting and responding to impacts on wallum sedgefrogs caused by changes in land use or climate. The negative relationship with eastern sedgefrogs supports the hypothesis that competition from eastern sedgefrogs is the mechanism that limits occurrence of wallum sedgefrogs in higher pH wetlands. The modeling framework that we developed for our study can be applied to improve management of other species exposed to anthropogenic threats including climate change.

Key words: acid frog; conservation; ecological niche; *Litoria olongburensis*; quantile regression; response model; wallum wetlands of eastern Australia.

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INTRODUCTION

In a changing environment, managers responsible for conservation of a threatened species need to know the environmental limits within which the species can continue to thrive (Huston

2002). This information is critical for understanding and predicting the impacts of anthropogenic threats, such as local land use and global climate change (Williams et al. 2008). The environmental limits of a species are typically the result of a combination of various abiotic and biotic

influences. A species' physiology can limit it to certain ranges of abiotic conditions, such as temperature and salinity, while biotic interactions that influence survival and reproduction, such as predation and competition, can exclude a species from otherwise suitable habitat (Hutchinson 1957, Huston 2002). The resultant subset of environmental conditions occupied by the organism is often called the realized niche (Hutchinson 1957) or ecological niche (Huston 2002).

When a species' limit is reached along a particular environmental gradient (e.g., a salinity gradient), a monotonic change in a species' abundance occurs. If the species' environmental tolerance is limited in two directions (i.e., it has upper and lower limits) along the gradient, abundance typically exhibits a unimodal response to the environmental factor (Westman 1980, Meents et al. 1983, Austin 2013). Selecting an appropriate response model is the key to accurate estimation of an environmental limit (ter Braak and Prentice 2004, Jansen and Oksanen 2013). Huisman et al. (1993) provide an approach for selecting the most likely response model from a set of models that are supported by ecological theory, including the logistic S-shaped and Gaussian bell-shaped curves. However, they model the mean response of the species, which is problematic when multiple environmental factors influence the species' response. Multiple regression is often used to model mean response to multiple environmental factors, and can provide basic information about responses to those factors (e.g., Meents et al., 1983, ter Braak and Looman 1995), but a model produced by multiple regression is unlikely to be useful for predicting environmental limits because it is often not possible to correctly identify and measure all limiting factors, nor correctly determine the form of response for every limiting factor, especially where the response is non-linear. An alternative method for dealing with multiple limiting factors is to model maximum response, using quantile regression (Koenker and Bassett 1978), instead of mean response. This approach enables more accurate prediction of a species' true response to an individual environmental factor (Cade et al. 1999, Guisan et al. 2006, Austin 2007), while eliminating issues that arise from modeling mean response (e.g., Johnson and VanDerWal 2009). A response model given by this method can therefore be expected to produce

more reliable estimates of environmental limits. Consequently, we have modified the methodology of Huisman et al. (1993) (hereafter referred to as HOF model selection) by testing the fit of models to maximum response, instead of mean response.

We use our novel version of HOF model selection to investigate environmental limits of the threatened species, *Litoria olongburensis* (wallum sedgefrog), which is restricted to naturally acidic wetlands in the coastal sandy lowlands ("wallum") of subtropical eastern Australia (Ingram and Corben 1975, Meyer et al. 2006). Land development in, and adjacent to, areas occupied by the frog is the main cause of its decline, while climate change is emerging as a new threat (Meyer et al. 2006). The wallum sedgefrog is one of four species Ingram and Corben (1975) called "acid frogs of the Wallum," due to the ability of their eggs and tadpoles to survive and develop in waters that are much more acidic than usual (pH < 5). Ingram and Corben (1975) hypothesized "acid frogs" could be excluded by other frogs in the event of sympatry, i.e., in waters with pH high enough to be occupied by the other species. Also, wallum sedgefrogs are thought to breed primarily in ephemeral or semi-permanent waters, rather than permanent waters (Ingram and Corben 1975, Ehmann 1997, Lewis and Goldingay 2005, Hines and Meyer 2011). Simpkins et al. (2014) provided quantitative evidence that the abundance of wallum sedgefrog tadpoles has a unimodal relationship with both pH and water depth (used as a proxy for hydroperiod). The limits of the species' ecological niche in relation to these environmental variables, or any others, have not yet been determined. Herein, we estimate the environmental limits of the species, and determine relationships with other biota that could explain existence of some limits. As well as providing guidelines for wallum sedgefrog conservation, we provide a modeling strategy that can be used to greatly enhance management and conservation of other species threatened by environmental change, including climate change.

METHODS

Field methods

We selected waterbodies to survey in localities spread throughout the geographic range of

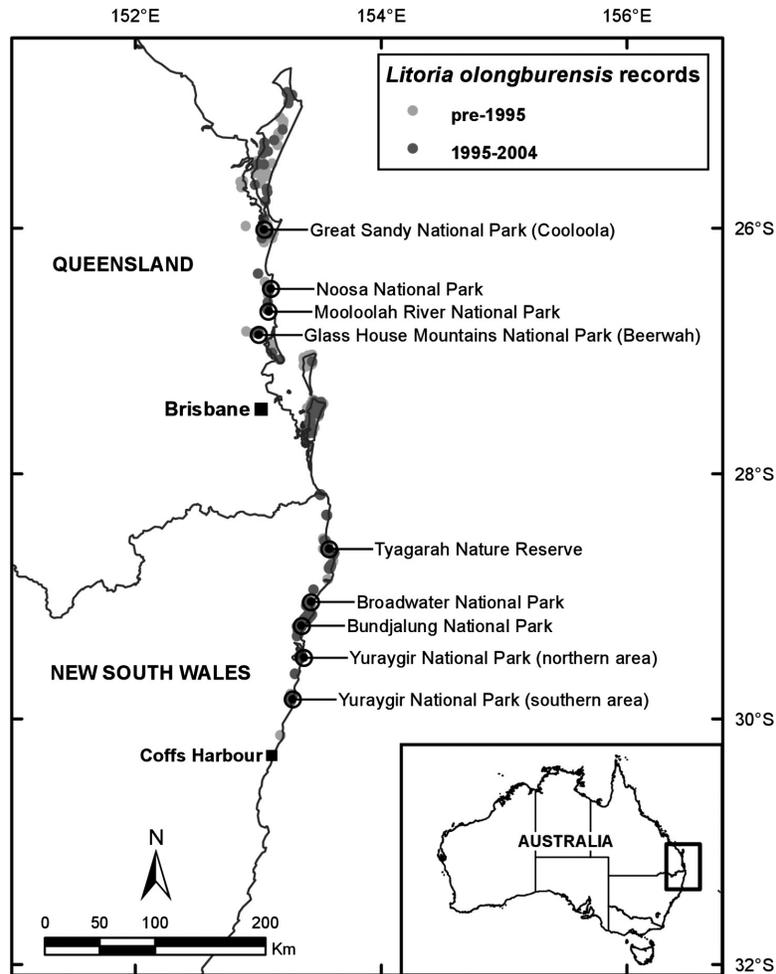


Fig. 1. Distribution of wallum sedgefrogs, and the nine areas surveyed in this study (source of records: Meyer et al. 2006).

wallum sedgefrogs on the Australian mainland (Fig. 1), as described by Shuker and Hero (2013). Line transects were used to sample each waterbody. For relatively small waterbodies ($n = 34$), a single transect crossed the waterbody from edge to edge, passing through the deepest part of the waterbody, or as near as practical (length = 25.5–200 m). For larger waterbodies ($n = 4$), a single edge-to-edge transect was not practical. Each of these larger waterbodies had two or three distinct vegetation zones, so a transect was placed in each vegetation zone, perpendicular to the vegetation gradient (length = 50–200 m). Abiotic characteristics, vegetation and aquatic predators were sampled at five equally spaced points (“sampling points”) along

each transect, except for one transect where time permitted only three sampling points. This transect had only minor variation in vegetation community composition, so three samples were considered sufficient. Water pH, salinity, temperature, turbidity, and depth were measured as described by Simpkins et al. (2014). Upright sedge cover was measured as described by Shuker and Hero (2013). Aquatic predators were sampled using a dip-net and fish-trap at each sampling point where possible. Five transects had insufficient water for any dip-netting, while 15 transects had insufficient water for fish-traps. Dip-net samples were collected as described by Simpkins et al. (2014). Each fish-trap consisted of a collapsible wire-framed mesh trap with 5.1 cm ring

openings at each end (“Surecatch” by Wilson Fishing, Tingalpa, Australia), baited with 5–6 mm food pellets (“Floating Fish Pellets” by Orca, Taiwan) and set for 45 min. Each transect was surveyed for frogs at night by two persons walking the transect centerline and recording individual frogs seen within 1 m on each side, as described by Shuker and Hero (2013). We also stopped at each of the aforementioned sampling points to record individuals calling within a 5 m radius during a 3-min period. The frog surveys commenced at least 30 min after sunset and ended prior to midnight.

All waterbodies were surveyed during March, 2010. Wallum sedgefrogs predominantly breed during the warmer and wetter months of the year, so their level of activity and reproduction during March is likely to be high (Ehmann 1997, Lowe et al. 2015). All areas received substantial rain (0.22–0.40 m at nearby weather stations) during the 30 d prior to surveys, providing wetland inundation necessary for the frog’s breeding activity (Lowe et al. 2015). Rainfall for the 12-month period prior to surveys was not unusually low for any area, although the second half of 2009 was substantially drier than normal in the Mooloolah River and Cooloola areas. These two areas each contained a wetland that was recovering from fire. The Mooloolah River wetland partially burned 6 months prior to our survey (Lowe et al. 2013), and the Cooloola wetland also appeared to have burned < 1 yr prior to our survey. In both cases, vegetation regrowth was sufficient to suggest that the wetland had largely recovered. Furthermore, monthly surveys of the burnt portion of the Mooloolah River wetland by Lowe et al. (2013) showed rapid recovery of the wallum sedgefrog population after the fire, such that fire would not have affected our measured values adversely.

Data analysis

Visual counts for all frog species on transects were standardized to 100 m². Juveniles were excluded because their abundance could be highly dependent upon precise timing of spawning at each location. *Crinia signifera* (common froglet) and *Crinia tinnula* (wallum froglet) were detected much more successfully during call surveys than visual surveys, so our measure of relative abundance for these two species was the average number of individuals calling at

survey points on each transect. *Litoria cooloolensis* (Cooloola sedgefrog) was excluded because its distribution range only encompassed our Cooloola sites (Meyer et al. 2006). Abundances of potential aquatic predators were standardized to catch per unit of effort (CPUE)—i.e., average count per point sampled—to account for absence of sampling at points with insufficient water. For fish, dip-net and fish-trap capture rates were summed for each waterbody, since dip-netting was not sufficiently effective on its own for capture of fish. For other potential aquatic predators (all invertebrates), only dip-net sampling was needed. For each transect, measurements of water characteristics and upright sedge cover at sampling points were averaged, with end-point samples half-weighted because they represent half the length of transect represented by other samples. The turbidity-tube measurements were used to ensure no waterbodies had high levels of suspended particulate matter (SPM), since high SPM can influence abundance of some frog species (Knutson et al. 2004). A turbidity tube does not distinguish between SPM and dissolved organic matter (DOM) that colors water (Dahlgren et al. 2004), so our turbidity tube measurements were potentially influenced by both SPM and brown-colored forms of DOM that cause acidity in wallum waters (Bayly 1964). However, a low value given by the turbidity tube can be taken to indicate the SPM level is low or zero.

For the four large waterbodies that require more than one transect, measures for each waterbody were calculated using weighted means of measures for transects in the waterbody. The weighting for each transect was the estimated proportion of the waterbody represented by the vegetation community on the transect. For three of the four waterbodies, these proportions were estimated using relative distances between GPS points recorded at the edges of the vegetation communities. The other large waterbody (in Mooloolah River National Park) was unable to be measured this way due to its large size and irregular shape. We estimated that the two transects in this waterbody represented the respective vegetation communities equally, based on visual assessment. For analysis of response to pH, the three transects in one of the large waterbodies were, however, treated as separate waterbodies

Table 1. Hierarchical set of models tested, in order of increasing complexity.

Response shape	Equation	Starting values
No response	$y = c$	Not required
Straight line	$y = mx + c$	Not required
S-shaped (logistic)	$y = a / (1 + e^{((x_{\text{mid}} - x)/s)})$	$x_{\text{mid}}: (x_{\text{min}} + [x_{\text{max}} - x_{\text{min}}])/2$ $s: \pm [x_{\text{max}} - x_{\text{min}}]/y_{\text{max}}$ $a: y_{\text{max}}$
Unimodal (Gaussian)	$y = y_{\text{peak}} \times e^{-\frac{1}{2} \times ((x - x_{\text{peak}})/\sigma)^2}$	$x_{\text{peak}}: x\text{-value at } y_{\text{max}}$ $\sigma: [x_{\text{max}} - x_{\text{min}}]/4$ $y_{\text{peak}}: y_{\text{max}} - y_{\text{min}}$

Notes: c is constant, m is slope, a is asymptotic value for the logistic curve, x_{mid} is value of x at point of inflection, s is scale at x_{mid} , y_{peak} is the value of y at the peak of the Gaussian curve, x_{peak} is value of x at y_{peak} , and σ is standard deviation. Starting values of parameters for non-linear regressions were calculated using the formulae shown.

because pH differed considerably among them, making it inappropriate to average pH of the transects. The differences in pH suggest connectivity of waters between transects was limited.

For each of our environmental measures, we tested a hierarchical set of models with increasing complexity using the approach of Huisman et al. (1993), and Jansen and Oksanen (2013). Following their approach, the simplest model is considered to best estimate the true response for a species if other more complex models do not fit the data better according to information criteria. Table 1 shows the forms of response we tested, and the corresponding equations we used. Our equations differ from those used by Huisman et al. (1993) because they modeled probability of occupancy, whereas we required equations suitable for modeling relative abundance. The equations we used also incorporate parameters that enable estimation of environment limits. The logistic equation (S-shaped response) gives an estimate of the point of inflection (x_{mid}), while the Gaussian equation (unimodal response) gives estimates of optimum (x_{peak}) and standard deviation (σ). These parameters indicate tolerance limits along the environmental gradient (ter Braak and Prentice 2004). The symmetric Gaussian model was the only form of unimodal response we considered because information regarding the suitability of more complex forms of unimodal response, such as skewed forms, for vertebrate species is lacking. Fitting a more complex form of response without evidence of suitability would risk over-fitting the data. We included a straight line model since it can more readily detect a response where the response range is only

partially captured by the sample, e.g., a segment of a logistic response (Meents et al. 1983). Also, instead of fitting models to the mean response of the study species to each variable of interest, we used quantile regression (Koenker and Bassett 1978) to investigate the species' maximum response. Modeling maximum response using quantile regression is recognized as a comprehensive approach to predicting a species' biological response to an individual environmental factor (Huston 2002, Guisan et al. 2006, Austin 2007). Relative abundance is one of many biological responses that can be modeled using quantile regression (e.g., Guisan et al. 2006, Vaz et al. 2008, Johnson and VanDerWal 2009, Petty et al. 2012). Given enough sample points, the biological response to an individual environmental variable can be estimated, even when other environmental factors are also influential, by fitting an appropriate response model to an upper quantile of the response data (Kaiser et al. 1994, Cade et al. 1999, Cade and Noon 2003, Guisan et al. 2006, Lancaster and Belyea 2006). For each environmental variable, we therefore fitted response models to the highest quantile possible for the data.

Abiotic environmental variables examined were mean pH, maximum depth, salinity and temperature of waterbodies, while biotic variables were upright sedge cover, relative abundance of other frog species that occupied four or more waterbodies, and relative abundance of aquatic predators that occupied four or more waterbodies. For each biotic variable, waterbodies with values of the biotic variable and wallum sedgefrog density both equal zero were excluded from the analysis so waterbodies unsuitable

Table 2. Response models that best predict the highest quantile (τ in 0–1) of wallum sedgefrog density in relation to environmental variables.

Variable	Response model	τ	Δ AIC	Model parameter	Estimate \pm SE	<i>t</i>	<i>P</i>
Acidity (pH)	Gaussian	0.89	18.7	Optimum	4.07 \pm 0.12	35.10	<0.001
				Tolerance	0.54 \pm 0.11	4.96	<0.001
				Asymptote	7.34 \pm 2.00	3.66	<0.001
Maximum water depth (cm)	Gaussian	0.88	12.9	Optimum	34.7 \pm 3.5	9.85	<0.001
				Tolerance	11.3 \pm 3.5	3.26	0.003
				Asymptote	8.8 \pm 2.2	4.00	<0.001
Eastern sedgefrogs (per 100 m ²)	Straight line	0.84	2.57	Slope	-1.34 \pm 0.43	-3.10	0.004
				Intercept	5.42 \pm 1.39	3.90	<0.001
Common froglets (per point)	Straight line	0.85	5.35	Slope	-1.81 \pm 0.47	-3.82	<0.001
				Intercept	5.42 \pm 1.42	3.82	<0.001
Wallum froglets (per point)	Straight line	0.85	4.76	Slope	-3.76 \pm 1.82	-2.07	0.048
				Intercept	5.92 \pm 1.45	4.07	<0.001
Oxleyan pygmy perch (CPUE)	Straight line	0.77	18.6	Slope	2.86 \pm 0.32	8.84	<0.001
				Intercept	4.49 \pm 0.71	6.31	<0.001

Note: Δ AIC is the difference in Akaike's Information Criteria relative to the null response model.

for both groups of organisms did not influence model selection. Response to each potential aquatic predator was tested only for waterbodies with sufficient water for sampling that fauna. For each environmental variable, the response models (Table 1) were compared using the Akaike's Information Criteria (AIC), with difference (Δ AIC) ≥ 2 taken to indicate superiority of the model with lower AIC (Burnham and Anderson 2002). For each response model, significance of relationships between each model parameter and the response variable was assessed ($\alpha = 0.05$). Starting values of parameters for non-linear regressions are included in Table 1. Outlier values for the response variable are not of concern since regression quantile estimates, unlike least-squares regression estimates, are not sensitive to them (Cade et al. 1999). Computations were completed in R (R Development Core Team 2014) with the *quantreg* package (version 5.05).

RESULTS

Wallum sedgefrogs were recorded in 28 (73.7%) of 38 waterbodies surveyed. Maximum relative density was 10.8 adults/100 m². Within each locality, wallum sedgefrog density varied considerably among waterbodies, except in the southern-most locality where densities were all low (0–1.33 adults/100 m²; $n = 4$) (Appendix S1: Fig. S1). Turbidity levels for all waterbodies were low (0–47 ntu). Mean acidity ranged from

pH 2.68 to 4.95, with three transects of a large waterbody in Bundjalung National Park being treated as separate waterbodies for the pH analysis due to the substantial differences in their pH (pH 3.58, 4.34, and 4.80 respectively). The unimodal (Gaussian-shaped) response model best predicted the highest quantile of wallum sedgefrog density for the pH gradient, with all the model's parameter estimates being statistically significant (Table 2, Fig. 2a). The model indicates wallum sedgefrogs are likely to be less abundant outside the range of pH 3.53–4.61 (± 0.11) (Table 2). Of the 20 waterbodies with pH within this tolerance range, only one (5%) had no wallum sedgefrogs detected. Outside the tolerance range, 10 waterbodies (50%) had no wallum sedgefrogs detected. Maximum water depth of waterbodies ranged from 5 to 48 cm. The Gaussian-shaped model also best approximated wallum sedgefrog density in relation to maximum water depth (Table 2, Fig. 2b). The model indicates wallum sedgefrogs are less likely to be detected in waterbodies with maximum depth outside the range 23.4–46.0 (± 3.5) cm (Table 2). All 15 waterbodies with maximum water depth in this tolerance range were occupied by wallum sedgefrogs. Of the 22 waterbodies with maximum depth below this tolerance range, 10 (45.5%) had no wallum sedgefrogs detected. Only one waterbody had maximum depth above the tolerance range, and it was occupied by wallum sedgefrogs.

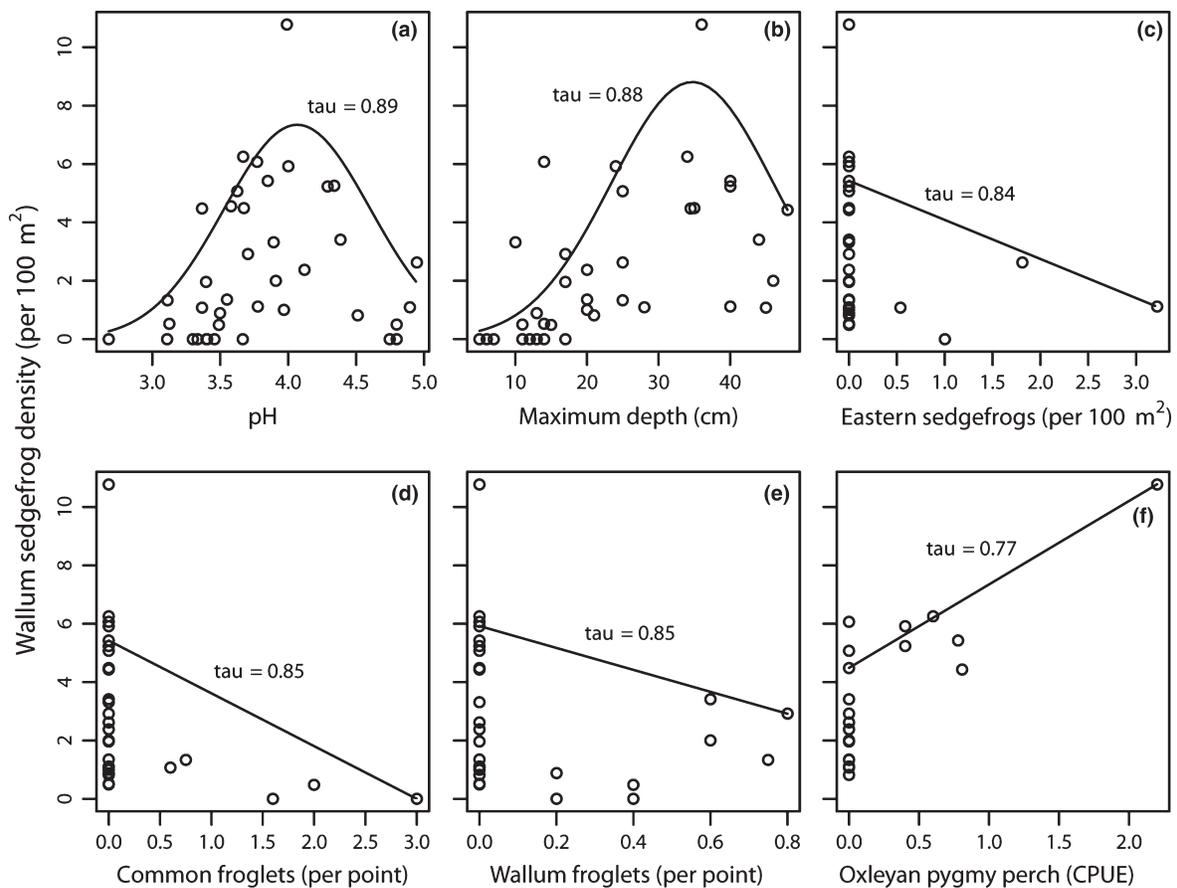


Fig. 2. Response models that best approximated the highest quantile of adult density for wallum sedgefrogs in relation to: (a) pH, (b) maximum water depth, (c) eastern sedgefrogs, (d) common froglets, (e) wallum froglets, and (f) Oxleyan pygmy perch. The τ -value shown for each variable was the highest possible for the data.

Wallum sedgefrogs were found across almost the full range of salinities (35.7–149 ppm; mean = 68.4 ppm) and water temperatures (20.1–28.4°C; mean = 24.2°C) of the waterbodies. Upright sedge species cover for the waterbodies ranged from 0 to 82.6% (mean = 28.3%), with only one waterbody having 0% cover. The highest wallum sedgefrog densities spanned almost the entire range of upright sedge species cover. None of the response models approximated maximum wallum sedgefrog density better than the “No response” model for salinity, water temperature or upright sedge species cover.

Nine other frog species were recorded during our surveys, with wallum froglets, common froglets, *Litoria fallax* (eastern sedgefrogs), and *Litoria freycineti* (wallum rocketfrogs) being the only species recorded in four or more waterbodies

(Table 3). Detection of wallum rocketfrogs was very low, with only one individual recorded in each of the five waterbodies in which the species was found. In seven waterbodies, no individuals of any frog species were observed during either the visual line survey or the point call surveys. In four of those seven waterbodies, one or more frogs were observed opportunistically, outside the time of the surveys. A decreasing straight-line model best approximated maximum wallum sedgefrog density in relation to relative abundance of each of three frogs—wallum froglets, common froglets and eastern sedgefrogs—indicating wallum sedgefrog density declines with increasing abundance of each of those frogs (Table 2, Fig. 2c–e). In relation to wallum rocketfrogs, none of the response models approximated maximum wallum sedgefrog density better than the “No response” model.

Table 3. Occupancy and maximum relative abundance of potential competitors and predators of the aquatic stages of wallum sedgefrogs.

Species/taxon	Sampling method	Occupancy		Maximum relative abundance
		<i>n</i>	%	
Wallum froglet	Call survey	9	23.7	0.80/point
Common froglet	Call survey	5	13.2	3.00/point
Eastern sedgefrog	Visual survey	4	10.5	3.22/100 m ²
Wallum rocketfrog	Visual survey	5	13.2	0.88/100 m ²
Oxleyan pygmy perch	Fish-trap + dip-net	6	26.1	2.20 CPUE
Firetail gudgeon	Fish-trap + dip-net	4	17.4	2.67 CPUE
Crayfish	Dip-net	22	66.7	1.80/point
Shrimp	Dip-net	5	15.2	3.95/point
Odonate nymphs	Dip-net	6	18.2	0.80/point
Aquatic beetles	Dip-net	25	75.8	9.60/point
Water boatmen	Dip-net	15	45.5	4.67/point
Fishing spiders	Dip-net	11	33.3	1.00/point

Notes: Aquatic fauna observed in four or more waterbodies are shown. For surveys conducted using point transects, relative abundance is the average number of individuals observed per point. CPUE is the sum of individuals dip-netted per point and individuals fish-trapped per point. Where dip-net or fish-trap sampling was used, percentage occupancy is the percentage of waterbodies able to be sampled, i.e., waterbodies not sampled due to insufficient water are excluded.

Potential aquatic predators captured most often by dip-net were crayfish (Decapoda: *Cherax* spp.), shrimp (Decapoda: *Atyidae* and *Palaemonidae* spp.), odonate nymphs (Odonata), aquatic beetles (Coleoptera), water boatmen (Corixidae), and fishing spiders (Pisauridae: *Dolomedes* spp.) (Table 3). With the combination of dip-net and fish-traps, fish were captured in 11 (47.8%) of the 23 waterbodies with sufficient water for deployment of fish-traps. Wallum sedgefrogs were recorded in all of the waterbodies that contained fish. The only fish species captured in four or more waterbodies were *Nannoperca oxleyana* (Oxleyan pygmy perch) and *Hypseleotris galii* (firetail gudgeons) (Table 3). The small, widely-distributed, non-native fish, *Gambusia holbrooki* (gambusia), was found in only two waterbodies—one in Yuraygir National Park (9.09 CPUE) and the other in Bundjalung National Park (17.8 CPUE). In both of those waterbodies, wallum sedgefrogs were also recorded (1.11 and 4.43 per 100 m² respectively). For Oxleyan pygmy perch, an increasing straight-line model approximated maximum wallum sedgefrog density much better than all other models, indicating wallum sedgefrog density increases with increasing abundance of Oxleyan pygmy perch (Table 2, Fig. 2f). For all other potential aquatic predators, none of the response models performed better than the “No response” model.

DISCUSSION

We used a novel combination of modeling techniques to obtain estimates of critical environmental tolerances for a threatened species, together with predictions of interactions with other fauna. Our results are consistent with the majority of observations reported in the literature for wallum sedgefrogs, giving credibility to the estimates and predictions of the modeling. These results can aid the decision-making of planners and managers responsible for conservation of the species, which is threatened by anthropogenic processes, including climate change. Wallum sedgefrogs are often described as occurring in “low” pH waters, and so an upper limit to pH tolerance has long been suspected (e.g., Ingram and Corben 1975, Lewis and Goldingay 2005, Anstis 2013). Hence, it is unsurprising that wallum sedgefrogs in our study appear to prefer waters with relatively low pH. However, the possibility of a lower limit on pH tolerance, in addition to an upper limit, has rarely been considered in previous studies of wallum sedgefrogs and other “acid frog” species. We previously reported a unimodal response to pH for relative abundance of wallum sedgefrog tadpoles, which were also sampled during surveys for the present study (Simpkins et al. 2014). Our modeling results herein indicate a unimodal response for adults,

as well, indicating existence of both lower and upper limits along the pH gradient. We were also able to predict a tolerance range for the species, which was not possible in the tadpole study. Our results indicate wallum sedgefrogs are less tolerant of waterbodies with pH outside the range 3.53–4.61 (± 0.11). This predicted tolerance range is consistent with pH levels reported for waterbodies occupied by embryos and larvae on Bribie Island, Queensland (Hines and Meyer 2011), and it encompasses the pH levels recorded for all six waterbodies occupied by wallum sedgefrogs adjacent to the Queensland–New South Wales border (M. C. Hopkins, *unpublished data*). Ehmann (1997) reported occurrence of wallum sedgefrogs in waters with pH ranging from 4.2 to 7.2 in far northern New South Wales, but provides no details to indicate whether occurrence at the higher pH levels was common or not.

Reduced abundance of wallum sedgefrogs below the predicted pH tolerance range could be due to physiological limitation, despite the species being one of the “acid frogs”, which tolerate lower pH than other anurans (Ingram and Corben 1975, Meyer 2004, Barth and Wilson 2010). Adaptation to low pH in “acid frogs” is suggested to include gills and integument with higher mucous levels and closer apposition of epithelial cells (Meyer 2004). Such adaptations might not be effective at the lowest pH levels that occur in wallum waters, causing abundance, and the likelihood of occurrence, to be reduced at the lowest pH levels we encountered. At the other end of the pH gradient, reduced abundance above the pH tolerance range could be caused by niche overlap with a competitor. Abundance and distribution of an anuran species can be limited by competition from other anuran species, particularly during the larval stage (e.g., Wilbur 1987). Ingram and Corben (1975) hypothesized that “acid frogs” might be excluded by other frogs in the event of sympatry, and our results are consistent with this hypothesis. In particular, our results indicate wallum sedgefrog density decreases with increased density of eastern sedgefrogs. Tadpoles of the eastern sedgefrog are unlikely to survive in the most acidic waters occupied by wallum sedgefrogs (Meyer et al. 2010), but they might outcompete wallum sedgefrog tadpoles in less acidic waters. Larval development time for

the two species is likely similar (Anstis 2013), so both species could be in competition for the same wetland if pH is high enough for eastern sedgefrogs. Sampling more wallum waterbodies inhabited by eastern sedgefrogs is required to determine its distribution along the pH gradient. If an upper pH limit occurs for wallum sedgefrogs due to competition from eastern sedgefrogs, it will coincide with the eastern sedgefrog’s physiological pH limit. We were unable to estimate pH tolerance for the eastern sedgefrog because they occupied only four waterbodies surveyed. Our analysis also indicated wallum sedgefrog density decreases with increasing density of both common froglets and wallum froglets. These two negative relationships could however be due to differing hydroperiod requirements, rather than competition. Larval development times for common froglets and wallum froglets are as little as about six and seven weeks, respectively, whereas development time for wallum sedgefrogs is estimated to be about 12 weeks (Anstis 2013, Lowe et al. 2015). Therefore, negative relationships with the two froglet species could be a consequence of the froglets occupying waterbodies with hydroperiod too short for development of wallum sedgefrog larvae into their terrestrial adult form.

Our results indicate that wallum sedgefrogs are less tolerant of waterbodies with maximum water depth outside the range 23.4–46.0 (± 3.5) cm. Wallum sedgefrogs are thought to occur primarily in relatively shallow swamps with ephemeral or semi-permanent waters (Ingram and Corben 1975, Ehmann 1997, Lewis and Goldingay 2005). Ephemeral waterbodies must however be deep enough to avoid desiccation before the aquatic eggs and larvae have had time to develop and metamorphose (e.g., Wilbur 1987). In our study, the lower densities of wallum sedgefrogs in waterbodies with maximum water depth below the predicted tolerance range could be due to those waterbodies being less likely to hold water long enough for eggs and tadpoles of wallum sedgefrogs to fully develop. At the other end of the depth gradient, the lower densities we found in waterbodies with maximum depth greater than the predicted tolerance range could be due to those waterbodies being more likely to hold water long enough to be occupied by aquatic fauna that consume anuran eggs and tadpoles. Anuran abundance and distribution

are often limited by predation on their eggs or larvae by aquatic fauna, such as fish (e.g., Hecnar and McLoskey 1997, Hero et al. 2001), odonate larvae (Smith 1983), and belostomatids (Ohba and Nakasuji 2006). However, we did not detect evidence of wallum sedgefrogs being limited by aquatic predators we sampled. We were able to analyse the response of the frog's relative density to two fish species, Oxleyan pygmy perch and firetail gudgeons, and a number of predatory invertebrates, including odonate nymphs, and found it to be unlikely that any of these biota limit the frog. Interestingly, wallum sedgefrog density appears to have a strong positive relationship with relative abundance of Oxleyan pygmy perch, suggesting these two species share very similar habitat dependencies. With regard to firetail gudgeons, our result is consistent with the observation of Hines and Meyer (2011), on Bribie Island, Queensland, that larval wallum sedgefrogs were often found sympatric with firetail gudgeons. We also captured *Gobiomorphus australis* (striped gudgeon) and gambusia, but were not able to analyse response to each of these species because they were captured in too few waterbodies. The low occurrence of striped gudgeons and gambusia at our sites might be due to low survivability in low pH waters. Also, striped gudgeons are a relatively large fish that might be restricted to waterbodies deep enough to hold water permanently. It is possible only a few of the waterbodies we sampled were permanent. We therefore suggest sampling more wallum waterbodies with maximum depth greater than our predicted optimum, so the possibility of striped gudgeons limiting wallum sedgefrogs in deeper, permanent waters can be investigated.

Salinity levels of all waterbodies we sampled were well below levels reported to influence survival and reproduction of anurans (e.g., Christy and Dickman 2002, Chinathamby et al. 2006), so it was unsurprising that our analysis indicated salinity did not limit wallum sedgefrog abundance. Water temperatures were relatively high during our surveys, as expected given the relatively warm weather, so it was also unsurprising that we found no response to water temperature. We were however surprised that upright sedge cover did not appear to limit wallum sedgefrog abundance, given wallum sedgefrogs were found to perch on upright sedges in preference

to other substrate during the our surveys (Shuker and Hero 2013). One or more other factors must have been limiting wallum sedgefrog abundance to levels below the levels that availability of upright sedges would allow. Influence of upright sedge availability might become more apparent during periods of intense breeding activity, especially if calling males are territorial. The low levels of calling activity we observed indicate that breeding activity was low during our surveys. While we recognize that presence of upright sedges is likely important to wallum sedgefrogs, we caution against using the level of upright sedge cover to gauge the level of habitat suitability for wallum sedgefrogs unless its influence on wallum sedgefrog abundance is demonstrated.

Conservation management implications

The mainland areas in which wallum sedgefrogs occur are expected to continue experiencing rapid growth in human populations with consequent rapid rates of land development (Hutson et al. 2008, DECCW 2009). Effective assessment of potential impacts on wallum sedgefrogs from proposed land developments, and effective monitoring and control of impacts from approved developments, are therefore particularly important. In addition to direct loss of habitat through clearing for land development, degradation of habitat might occur if chemistry or volume of water flowing into the habitat changes as a result of development in an adjoining catchment area (Meyer et al. 2006). Habitat could also be lost or degraded due to ongoing climate change. In Australia's East Coast region, which contains all wallum sedgefrog populations, average temperature is predicted to rise, with the hottest days being hotter and more frequent, and evaporation rates also rising (Dowdy et al. 2015). Rainfall change in the region is unclear, apart from reduced winter rainfall in southern areas and increased intensity of heavy rainfall events (Dowdy et al. 2015). The predicted changes in temperatures and rainfall could severely alter suitability of wetlands available to wallum sedgefrogs. For example, increased evaporation and reduced rainfall would likely cause longer and more frequent desiccation of wallum wetlands. Changes in rainfall might also impact on water pH in the wetlands. If these changes reduce availability of wetlands with suitable hydroperiod

and pH for wallum sedgefrog reproduction, their populations will likely decline. The optimal pH levels and water depths suggested by our results provide a necessary baseline for predicting and responding to impacts resulting from changes in climate or land use. In addition, the findings provide guidance for construction of habitat, such as “compensatory” ponds built where habitat has been destroyed for land development (e.g., EcoPro Pty Ltd 2004), or in response to climate change (Shoo et al. 2011). For example, our results suggest that the success of a constructed pond would depend on whether suitable acidity and hydroperiod can be achieved.

Our study also has implications for management of threatened species in general. Around the world, many species are, like wallum sedgefrogs, in decline due to environmental change caused by human activities (Hoffmann et al. 2010). Understanding a species’ environmental limits is essential in predicting whether environmental change will cause decline of the species. However, determination of environmental limits for threatened species is often problematic. Using controlled experiments in the field or in a laboratory is often restricted by practical and ethical issues. Here, we provide a novel framework for quantifying the abiotic and biotic limits of a species using field observations. We improved the hierarchical model selection approach of Huisman et al. (1993) by modeling maximum response to an environmental factor, instead of mean response, to eliminate issues that arise when one or more other environmental factors also influence the response. Given comprehensive sampling across a range of environmental conditions that encompass the species’ environmental limits, a conservation manager can apply our model selection method to determine an appropriate response model for the species, and then use this model to predict environmental limits. Increasing the number of samples, as well as the spread of samples along the environmental gradient, will enable closer approximation of the response to the environmental factor being examined, and subsequently will allow more accurate prediction of an environmental limit that occurs along the gradient. Knowledge of environmental limits can then be used to guide monitoring of habitat for change that would threaten survival of the species, and inform actions taken to maintain suitability of its

habitat or construct compensatory habitat when existing habitat is lost.

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