Urbanization interferes with the use of amphibians as indicators of ecological integrity of wetlands

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Summary

1. Wetlands are ecologically and economically important ecosystems but are threatened globally by many forms of human disturbance. Understanding the responses of wetland species to human disturbance is essential for effective wetland management and conservation.

2. We undertook a study to determine (i) whether anurans can be used effectively to assess the ecological integrity of wetlands affected by groundwater withdrawal and, if so, (ii) what effect increasing urbanization might have on the utility of anurans as wetland indicators. We monitored the intensity of anuran calls at 42 wetlands in south-western Florida throughout 2001–2002 and 2005–2009.

3. We first validated the use of anurans to assess wetland integrity using a small group of wetlands by comparing anuran calling and subsequent tadpole development with an established index employing vegetation composition and structure. We then verified that the results could be expanded to a variety of sites throughout the region. Finally, we focused on urbanized wetlands to determine whether urbanization could interfere with the use of anurans to assess wetland integrity.

4. We used PRESENCE to estimate occupancy and detection probabilities and to examine the relationship between occupancy and five covariates expected to influence individual species occurrence. We used FRAGSTATS to calculate the mean proximity index for urbanized wetlands, which assesses the size and distribution of land use types within a specified area.

5. Our results showed that the group of species including oak toad Anaxyrus quercicus, southern cricket frog Acris gryllus, pinewoods treefrog Hyla femoralis, barking treefrog Hyla gratiosa, and little grass frog Pseudacris ocularis is a reliable indicator of wetland integrity. However, this same group of species, which is sensitive to wetland health, is selectively excluded from urbanized wetlands.

6. Synthesis and applications. Although anurans are effective indicators of wetland health and complement vegetation surveys, the usefulness of this group for monitoring the ecological integrity of wetlands can be substantially reduced, or eliminated, as a consequence of urbanization. We urge for careful consideration of confounding factors in any studies examining the utility of indicator species.

Key-words: anuran, bioindicators, fragmentation, groundwater withdrawal, mean proximity index, uplands, urbanization, vegetative monitoring, wellfield

Introduction

A variety of biological indicators (insects, plants, birds, mammals, reptiles and amphibians) have been used with success in wetland habitats across regions in several countries (e.g. Findlay & Houlahan 1997; Welsh & Ollivier 1998; Jansen & Healey 2003; Lee Foote & Hormung 2005; Reiss 2006; Howe et al. 2007; Price et al. 2007). Our study focuses on understanding the responses of potential wetland indicator species, specifically amphibians, to groundwater withdrawal, as indicators...
are essential to the effective management of wetlands. The composition of amphibian assemblages is influenced by changes in physical conditions of wetlands, such as the alteration of hydrologic regimes (Vickers, Harris & Swindel 1985; Skelly 1996). Alteration of hydrologic regimes by excessive groundwater withdrawal has been shown to affect anurans (Guzy, Campbell & Campbell 2006; Bunnell & Ciraulo 2010), and their responses might be immediately noticeable in some species on a local scale, especially regarding the breeding effort. While calling surveys in a given year may not reflect the actual population size of anurans, which can often survive years of catastrophic reproductive failure (Petranka et al. 2007), they can reflect wetland condition, as reproductive effort is completely dependent on water.

The composition and structure of wetland vegetation are often used as indicators of wetland degradation from excessive groundwater withdrawal (Sonenshein & Hofstetter 1990; Edwards & Denton 1993; Ormiston et al. 1995). Excessive withdrawal can lower the surface of the aquifer, which in turn can lower the surficial aquifer and finally the level of inundation in wetlands (Cherry, Stewart & Mann 1970; Stewart 1968; SWFWMD 1999). Many places that have the potential to suffer from excessive groundwater withdrawal have regulations to forestall the problem. In south-western Florida, a large area with thousands of wetlands, the ecological condition of wetlands within all wetland fields must be assessed annually (SWFWMD 2012), typically using a vegetative health rating (VHR), which incorporates several botanical and physicochemical measurements to rate wetlands according to the level of ecological damage caused by groundwater withdrawal (Gonzalez 2004). Although using a measure of vegetation composition and structure as an indicator of wetland condition is relatively easy, changes in vegetation are gradual (especially for shrubs and trees which may survive several poor years) and thus VHRs are indicators of relatively long-term effects. While changes in amphibian populations can also show short-term effects, amphibian calling activity coupled with the presence of tadpoles and near-metamorphs can give a current measure of wetland condition: disturbed wetlands may not attract breeding adults, and hydrology that is too altered will not sustain larval development through metamorphosis. As the use of groundwater resources increases in many places, a more rapid assessment of wetland condition is required, and anurans may be a valuable suite of indicators. Furthermore, if they are equal or more effective as indicators, anurans could provide an easier, more cost-effective and faster assessment than vegetation; this may be important given rapid human development of certain areas worldwide.

Urbanization currently threatens more than one-third of the world’s known amphibian species; the main threats are from habitat loss, fragmentation and degradation (Hamer & McDonnell 2008). Although some anurans move relatively long distances (1–6 km; Lemckert 2004), amphibians in general tend to have poor dispersal abilities (Semlitsch 2000) and dispersal distances typically are <0.3 km (Gibbs 1993; Semlitsch & Bodie 2003). As urban sprawl increases, dispersal corridors are likely to be disrupted, reducing amphibian richness because of increased fragmentation and degradation of wetlands (and the upland matrix between); this restricts the potential for migration among wetlands and limits recolonization of species to wetlands from which they have been extirpated. Thus, wetlands in urban settings have reduced amphibian species richness (e.g. Delis, Mushinsky & McCoy 1996).

Our objectives were to (i) conduct a long-term study of cypress domes in south-west Florida to evaluate the potential utility of anurans in providing a quick and reliable assessment of wetland decline resulting from groundwater withdrawal and (ii) to determine whether urbanization interferes with the ability to use anurans as indicators for excessive groundwater withdrawal.

Materials and methods

Sites and species data collection

Throughout 2001–2002 and 2005–2009, we monitored calling anurans at 42 cypress-dome wetlands, grouped within seven sites, in the Tampa Bay region of south-western Florida (Fig. 1a). During 2001 and 2002 (Study 1), we monitored 18 (10 ‘blue’, 5 ‘green’, and 3 ‘red’; see below for definition of these VHR ratings) wetlands at Starkey Wellfield (Fig. 1a), to determine whether wetland assessment based on calling activity of anurans was correlated with wetland assessment based on the VHR (Gonzalez 2004; SWFWMD 2012). A VHR rating of ‘blue’ is assigned to wetlands with vegetation, hydrology and soils indicative of a naturally functioning wetland (i.e. high ecological integrity); of ‘green’ to wetlands with moderate changes in vegetative composition and zonation, hydrologic indicators, and soil subsidence (‘moderately impacted’); and of ‘red’ to wetlands with severe changes in vegetative composition or zonation, treefall or death, soil oxidation or subsidence, and other biological evidence of hydroperiod reduction (‘highly impacted’) (Gonzalez 2004; Fig. 1b–d). A naturally functioning wetland is saturated by surface or groundwater at a frequency and duration sufficient to support a prevalence of vegetation adapted to saturated soils (EPA 2012). ‘Moderate’ vegetative changes occur when transitional species move from edges of a wetland into the deep zone and ‘severe’ changes occur when upland vegetation moves into the deep zone (SWFWMD 2012). Each wetland was monitored for calling anurans (described below) five to seven times each year, between May and September. Because intensity of calling anurans does not necessarily indicate the quality of wetland habitats for amphibian reproduction, we also sampled tadpoles in a subset of wetlands (5 ‘blue’, 5 ‘green’ and 3 ‘red’) to verify that wetlands had a sufficient hydroperiod to allow recruitment of tadpoles to the terrestrial stage. Each wetland was sampled for tadpoles using D-frame dip nets; up to 20 1-m sweeps were conducted in each microhabitat (vegetation or open water) proportional to the fraction of the total area each microhabitat covered. Passive sampling with traps (60 × 30 × 30 cm) was applied at each site with water at least 0.2 m deep. Tadpoles were identified to species and classified in Gosner Stage Categories (Gosner 1960); fish species and invertebrates (potential predators) were also recorded during dip-netting and trapping. Each wetland was monitored for tadpoles six to seven times each year, between July and December.

During 2005 and 2006 (Study 2), to determine whether the results of the earlier monitoring were generally applicable, we monitored a subset of four wetlands at Starkey Wellfield plus four wetlands each at three other sites (Cypress Creek, Cypress Bridge, and Morris...
Bridge; Fig. 1a), all actively pumped for groundwater and with varying levels of nearby urbanization. We also monitored four wetlands at another site, Green Swamp (Fig. 1a), with no groundwater withdrawal or surrounding urbanization. Each of the 20 wetlands was monitored 10 times each year, between May and September. During 2007, 2008 and 2009 (Study 3), we monitored the same 20 wetlands plus three additional wetlands each at two sites, Dale Mabry and Sheldon (Fig. 1), surrounded by extensive urbanization. Each of the 26 wetlands was monitored for calling anurans approximately one evening every 2 weeks, targeting rainfall events, from the end of May until the middle of September for a total of nine surveys each year. Call surveys were performed after sunset between 20:00–24:00 h and timed to coincide with the onset of calls in late spring and the end of the calling period in early fall.

During each calling anuran monitoring event throughout the study, simultaneous call surveys were conducted by two experienced researchers listening for 5 min from the centre of each wetland. All species present were listed, water depth was recorded and any differences in species observed were reconciled before leaving the wetland. Calling activity was measured in chorus size categories based on

Fig. 1. The 42 study wetlands in central Florida (a); and examples of a least-impacted (Blue VHR score) wetland (b), moderately impacted (Green VHR score) wetland (c), and a severely impacted (Red VHR scores) wetland (d). VHR, vegetative health rating.
North American Amphibian Monitoring Program (NAAMP 2011) guidelines, but refined to reflect the following six categories of numbers calling males: 1–10, 11–25, 26–50, 51–100, 101–500 and >500. Subsequently, the length of time that each wetland contained surface water (hydroperiod) was determined from water-level data recorded during call surveys, supplemented with data obtained from regulatory agencies. The influence of hydroperiod on amphibian occupancy is well-documented (e.g. Snodgrass et al. 2000; Beja & Alcator 2003), and highly ephemeral wetlands generally contain species with rapid development and conspicuous feeding, but wetlands with a relatively long hydroperiod contain more established predator populations, and thus slower growing, less conspicuous feeding species utilize these wetlands.

**LANDSCAPE DATA COLLECTION AND DATA ANALYSIS**

We measured a series of variables for each wetland in Study 3, by building a geographical information system in **arcmap**, v 9.3.1 (ESRI 2009), based on georeferenced digital 1 : 100 000 USGS geological Orthophoto Quarter Quadrangle maps of 2009 aerial photographs and National Wetlands Inventory shapefiles (SWFWMD 2010). These variables included (1) distance to nearest study wetland (indication of possible spatial dependence), (2) distance to nearest natural wetland, (3–5) per cent forest cover within 500, 1000 and 2000 m, and (6–8) mean proximity index (MPX) of forest cover within 500, 1000 and 2000 m; other measured variables included (9) average hydroperiod and (10) water depth at deepest point and (11–13) time (month, year or month plus year) as calling activity of anurans is strongly seasonal. One variable, MPX within 500, 1000 and 2000 m of the perimeter of each wetland, reflected the possible importance of urbanization and its consequent fragmentation. MPX assesses not only the amount of forest cover within a specified search radius, but also the distribution from clumped to uniform by measuring the isolation of each forest patch within a complex of forest patches (Gustafson & Parker 1992). Other metrics calculated within the same search radius (e.g. road density, proportion of impervious surfaces) do not take into account the spatial distribution. In our study, a ‘patch’ is defined as each individual occurrence of a particular land cover type (e.g. forest) in the landscape; the MPX approaches zero if a patch has no neighbours of the same patch type and increases as the neighbourhood is increasingly occupied by patches of the same type and as those patches become closer and more contiguous (or less fragmented) during Studies 1 and 2 for patterns of species’ co-occurrence. Groupings of species (using average calling index) and wetlands were identified with two-way cluster analysis, as implemented in **pcooR**, v 5 (McCune & Mefford 1999). The Bray–Curtis Index was used as the distance measure, and the group average method was used for linking groups. To test whether resulting groups of species and wetlands (not identified *a priori*) were significantly different from each other in multivariate patterns of co-occurrence across wetlands, we used the SIMPROF routine in **primer**, v 6 (Clarke & Gorley 2006). Co-occurrence patterns for individual species and also the relationship between individual species and VHR rating were identified by calculating Spearman rank correlations in **statistica** 7.1 (StatSoft 2005).

**OCCUPANCY MODELING**

Although detection of a species confirms its presence, lack of detection does not necessarily confirm absence. Thus, when detection probabilities are less than one, the true proportion of wetlands occupied should be estimated (e.g. MacKenzie & Kendall 2002). We used a single season mark–recapture-like approach (MacKenzie et al. 2002), as implemented in **preSENCE**, v 3.1 (Hines 2006), to estimate true proportion of sites occupied by each species for Study 3. We modelled detection probability and site occupancy as a function of different covariates according to the methods described by MacKenzie et al. (2002). Because collinearity between predictor variables can confound their independent effects, we calculated Spearman rank correlation coefficients for all pairwise combinations of independent variables (Hair et al. 1998); five of the 13 exploratory habitat variables (MPX, hydroperiod, water depth, time and distance to next study wetland) had correlation coefficients ranging between –0.04 and 0.31, with P-values above 0.05, and were included individually in subsequent modelling. The remaining inter-correlated variables were eliminated. Because MPX was strongly correlated between each buffer zone, we chose MPX at the 500-m buffer for subsequent modelling as the more biologically relevant variable when considering typical dispersal distances for most anurans. The resulting set of candidate models for each species were composed of one covariate each: (1) MPX within 500 m of the wetland, (2) distance to next study wetland, (3) average hydroperiod (each site specific predictors of occupancy), (4) water depth (survey specific predictor of detection) and (5–7) time-specific effects on detection (month, year or month plus year) for each species. Model selection was based on Akaike Information Criteria (AIC), which was adjusted for overdispersion and small sample sizes (i.e. QAICc) (MacKenzie & Bailey 2004). We computed delta QAICc and Akaike weights to determine the strength of evidence for each model (Burnham & Anderson 2002). Because it was impractical to summarize AIC results for all possible models for each species, we present the top 3–4 models and weights to gauge importance of each factor for each species. All continuous variables were standardized (i.e. the mean was subtracted from each value and then divided by the SD) before analysis.

We assumed models with higher weights, and lower AIC values were better able to explain variation in data and selected the models with substantial empirical support which included models within A2 QAICc (Burnham & Anderson 2002) and parameter estimates with standard errors not overlapping zero. We eliminated models where β coefficients of covariates were not supported.

**Results**

**ANURANS AS INDICATORS OF WETLAND CONDITION**

Linear regression analysis of Study 1 data indicated a significant (P = 0.001) positive relationship between average

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calling male size category and the average effort-corrected number of late-stage tadpoles at sites with increasing VHR score, and the model accounted for much of the variation ($R^2 = 0.67$; Fig. 2). Similarly, linear regression analysis indicated a significant ($P = 0.006$) positive relationship between average number of calling male species and the average number of tadpole species at sites with increasing VHR score and the model accounted for much of the variation ($R^2 = 0.51$; Fig. 3).

Cluster analysis of the Study 1 data revealed two significantly (SIMPROF, $\pi = 8.175$, $P < 0.05$) different groups of species (hereafter referred to as Group 1 and Group 2; Fig. 4). Group 1 is composed of five species: the oak toad *Anaxyrus quercicus*, southern cricket frog *Acris gryllus*, pinewoods treefrog *Hyla femoralis*, barking treefrog *Hyla gratiosa* and little grass frog *Pseudacris ocularis*. All five species in the group positively co-occurred ($r_S = 0.51-0.77$, all $P$-values <0.02). Group 2 is composed of six species: the southern toad *Anaxyrus terrestris*, squirrel treefrog *Hyla squirella*, green treefrog *Hyla cinerea*, eastern narrow-mouthed toad *Gastrophryne carolinensis*, pig frog *Lithobates sphenocephalus* and southern leopard frog *Lithobates catesbeianus*. All six species in the group also positively co-occurred ($r_S = 0.46-0.56$, all $P$-values ≤0.05). The remaining four species (southern chorus frog *Pseudacris nigrita*, greenhouse frog *Eleutherodactylus planirostris*, gopher frog *Lithobates capito* and bullfrog *Lithobates catesbeianus*) had limited occurrences and are not considered further. The occurrence of species in Group 1 exhibited a positive relationship with wetlands having a ‘blue’ VHR rating ($r_S = 0.50-0.79$, all $P$-values ≤0.04), but the occurrence of species in Group 2 did not exhibit any relationship to a particular VHR rating ($r_S = 0.06-0.44$, all $P$-values ≥0.18) (Fig. 4). Precisely the same two groups were identified by cluster analysis of Studies 2 and 3 data together (SIMPROF, $\pi = 6.89$, $P < 0.01$), and, once again, species within each group positively co-occurred ($r_S = 0.49-0.95$, all $P$-values ≤0.01, Group 1; $r_S = 0.38-0.85$, all $P$-values ≤0.05, Group 2). Blue wetlands clustered tightly together (SIMPROF, $\pi = 24.35$, $P < 0.01$; Fig. 4), but green and red wetlands did not group out reliably (Fig. 4).

**Fig. 2.** Linear regression of average calling male size category against the average effort-corrected number of tadpoles per site 2001–2002 ($R^2 = 0.67$, $P = 0.001$). Squares, triangles and circles represent Red, Green and Blue wetlands, respectively, as scored by the vegetative health rating. Dotted lines represent 95% confidence intervals.

**Fig. 3.** Linear regression of average number of calling male species against the average number of tadpoles species per wetland ($R^2 = 0.51$, $P = 0.006$). Squares, triangles and circles represent Red, Green and Blue wetlands, respectively, as scored by the vegetative health rating. Dotted lines represent 95% confidence intervals.

**EFFECTS OF URBANIZATION ON ANURAN INDICATORS**

Environmental variables differed markedly among wetlands (Table 1). With the exception of the Green Swamp (control site), all wetlands were located on sites with active groundwater withdrawal. All wetlands with high MPX values (within 500 m of the wetland) were located on large undeveloped wellfields or wilderness preserves and all were buffered from urban areas (Fig. 5); at Morris Bridge, Starkey Wellfield, Cypress Creek Wellfields and the Green Swamp, the nearest urban land cover ranged from 2.6 to 14.9 km away. Wetlands with low MPX values were located in areas immediately adjacent to urban land cover.

We present the results for the eight species with enough detections to allow occupancy models to converge and also provide standard errors not overlapping zero. Top models showed that occupancy varied by the inclusion or omission of MPX or water depth. The best models selected for the four of the five species previously identified as Group 1 (*A. quercicus*, *A. gryllus*, *H. femoralis* and *P. ocularis*) were very similar, as their pattern of co-occurrence would suggest; for all species, MPX within 500 m was identified as the best predictor for occupancy. Positive $\beta$ coefficients of covariates and occupancy estimates for each of these Group 1 species indicate that occupancy increases with increasing MPX (Table 2, Fig. 6). The best model for detection for each of these Group 1 species included a constant probability of occupancy over time (Table 2).

The best models selected for four of the six species previously identified as Group 2 (*A. terrestris*, *H. cinerea*, *G. carolinensis* and *L. grylio*) were also very similar. Water depth (a sample specific covariate) in study wetlands was the best predictor of detection for each of these species; positive $\beta$ coeffi-
coefficients of covariates for each of these Group 2 species indicate that detection increases with increasing water depth (Table 2; Fig. 7). The best model for occupancy for each of these species indicated a constant probability of occupancy over time (Table 2).

Probability of occupancy differed greatly between Groups 1 and 2. Species in Group 1 had a higher probability (0.6–1.0) of occupancy in sites with no or low levels of urbanization (MPX \(\leq 0.72\)) compared to that of sites with high levels of urbanization (MPX = 0.0–0.48; Fig. 6). For species in Group 2, probability of occupancy was not different in low, moderate and highly urbanized areas (i.e. no pattern was observed at differing MPX levels; Table 2).

**Discussion**

We identified a group of positively co-occurring species of anurans in cypress-dome wetlands that can indicate wetland health more rapidly than the commonly employed vegetative health assessment. The calling index of species in this group was highest in wetlands with the highest VHR. Coincidentally, these

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Table 1. Range of measured environmental variables among 26 wetlands sampled from 2007–2009

| Next study site (m) | Next natural wetland (m) | % Forest (500 m) | % Forest (1000 m) | % Forest (2000 m) | MPX (500 m) | MPX (1000 m) | MPX (2000 m) | Hydroperiod (days) | No. of sampling nights with rain | Water depth (cm) |
|--------------------|--------------------------|------------------|-------------------|------------------|-------------|-------------|-------------|-------------------|------------------|----------------|
| Mean               | 1880                     | 117-11           | 71                | 68               | 66          | 0.64        | 0.60        | 0.47              | 62               | 16             | 9.98          |
| Minimum            | 290                      | 10               | 13                | 12               | 17          | 0.01        | 0.05        | 0.01              | 0                | 13             | 0.00          |
| Maximum            | 5800                     | 377              | 100               | 100              | 100         | 1.00        | 1.00        | 1.00              | 206              | 21             | 73-15         |

Next study site = distance (m) from study wetland to the nearest on-site study wetland (n = 7 sites); Next natural wetland = distance (m) from a study wetland to the nearest natural wetland; % Forest = percentage of forest within 500, 1000 or 2000 m radius of perimeter of each study wetland; MPX = mean proximity index, amount and distribution of forest cover within 500, 1000, and 2000 m of the perimeter of each study wetland; Hydroperiod = mean number of days each wetland held water during sampling season each year; Water depth = depth of water in each wetland at every sampling occasion.
term efforts at multiple locations, particularly during droughts. To separate natural population variability from true population changes, and anuran larvae. Wetland plants have many characteristics suited to assessments of biological condition, including their relative immobility, well-developed sampling protocols and, for herbaceous species, moderate sensitivity to disturbance (Doherty et al. 2000). However, wetland plants are unreliable as sole indicators of change in hydrologic regime (Tiner 1991), and soil biogeochemistry should be used with vegetation to minimize lag times in plant response to hydrologic alteration; this is often cost prohibitive. Therefore, amphibians can be used as indicators to supplement ongoing vegetative and hydroperiod monitoring to provide a rapid response measure.

Our results suggest that certain calling anuran species can provide a superior method (compared with vegetation indexing), for the assessment of ecological integrity of wetlands that is accurate, rapid and can be applied at a large number of wetlands simultaneously. Calling surveys also appear superior to tadpole surveys, because they are substantially cheaper and less time-consuming for areas with large numbers of wetlands, and perhaps more reliable when overflow from permanent water bodies could act as a source of predatory fish. During our study, all wetlands were ephemeral, and any overflow events that introduced fish did so after tadpoles began metamorphing. The high degree of co-occurrence and predictive ability of the species in the group was maintained as the number of wetlands studied was increased. Thus, these species can be considered ‘sensitive’ to wetland degradation, in this case resulting from excessive groundwater withdrawal.

While amphibians can be useful indicators, it can be difficult to separate natural population variability from true population decline and thus anuran studies should be designed as longer-term efforts at multiple locations, particularly during droughts. In addition, adults may be in wetlands for a short time; however, their reproductive windows are well-established, generally easily targeted, and occupancy statistics can accommodate imperfect detection. Common problems that occur when using both vegetation and amphibians as indicators include misidentification and difficulties identifying dormant-season vegetation and anuran larvae. Wetland plants have many characteristics suited to assessments of biological condition, including their relative immobility, well-developed sampling

"healthy" wetlands supported the greatest species richness of anurans and were the only wetlands supporting the entire suite of species in the group. Because the intensity of calling anurans does not necessarily indicate the quality of wetland habitats for amphibian reproduction, we verified that these same wetlands had hydroperiods long enough to support tadpole development and found that the presence of late-stage tadpoles was strongly related to calling index. Thus, for all subsequent studies, we used data from calling anurans.

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Table 2. Best models for anuran species, based on parameter estimates and AIC selection criteria. Models were constructed from uncorrelated covariates. Best supported models are in bold.

| Species                  | Models                                     | No. of detections | QAICc | Δ QAICc* | w†  | K‡ | –2 log likelihood | Untransformed coefficients of covariates (standard errors) |
|--------------------------|--------------------------------------------|-------------------|-------|----------|-----|----|-------------------|----------------------------------------------------------|
| Anaxyrus quercicus       | Naïve estimate§: 0.42                      | 23                |       | 194.10   | 0.00| 0.75| 3               | 187.01                                                   |
|                          | $\Psi$(MPX), p(.), $\Psi$(.), p(Month)    | 198.15            | 4.05  | 0.10     | 3   | 191.06 | 0.62 (0.49) – 1.89 (0.51) – – – – 0.32 (0.19) |
|                          | $\Psi$(.), p( )                            | 198.60            | 4.50  | 0.08     | 2  | 194.08 | 0.72 (0.50) – 2.67 (0.27) – – – – – |
|                          | $\Psi$(Ave HP), p(.)                       | 200.67            | 6.57  | 0.03     | 3  | 193.58 | 0.96 (0.82) – 2.67 (0.27) – – 0.31 (0.22) – – |
| Anaxyrus terrestris      | Naïve estimate§: 0.15                      | 9                 |       | 85.42    | 0.00| 0.63  | 3  | 78.33 | –1.34 (0.63) – 3.51 (0.69) – 1.36 (0.61) – – – – |
|                          | $\Psi$(.), p(Water depth)                   | 87.86             | 2.44  | 0.19     | 2  | 83.34  | –1.54 (0.58) – 2.55 (0.42) – – – – – |
|                          | $\Psi$(.), p(Month)                        | 89.00             | 3.58  | 0.11     | 3  | 81.91  | –2.71 (1.32) – 2.55 (0.42) – 0.32 (0.28) – – – – |
|                          | $\Psi$(Ave HP), p(.)                       | 89.55             | 4.13  | 0.08     | 3  | 82.46  | –1.54 (0.58) – 3.18 (0.85) – – – – 0.08 (0.07) |
| Acris gryllus            | Naïve estimate§: 0.46                      | 68                |       | 367.68   | 0.00| 0.92  | 3  | 360.59 | –1.89 (0.86) – 1.33 (0.14) 3.49 (0.77) – – – – |
|                          | $\Psi$(MPX), p(.)                           | 373.31            | 5.63  | 0.06     | 2  | 368.79 | –0.39 (0.15) – 1.33 (0.14) – – – – – |
|                          | $\Psi$(.), p(Month)                        | 375.00            | 7.32  | 0.02     | 3  | 367.91 | –0.71 (0.68) – 1.33 (0.14) – – – – 0.17 (0.12) – |
| Hyla cinerea             | Naïve estimate§: 0.54                      | 74                |       | 98.86    | 0   | 0.96  | 3  | 367.06 | 0.42 (0.25) – 2.27 (0.22) – 1.43 (0.23) – – – – |
|                          | $\Psi$(.), p(Water depth)                   | 106.9             | 8.07  | 0.02     | 2  | 409.64 | 0.42 (0.25) – 1.41 (0.13) – – – – – |
|                          | $\Psi$(.), p(Ave HP)                       | 108.6             | 9.74  | 0.01     | 3  | 406.03 | 1.40 (0.86) – 1.41 (0.13) – 0.86 (1.05) – – – – |
| Hyla femoralis           | Naïve estimate§: 0.46                      | 59                |       | 312.31   | 0.00| 0.84  | 3  | 335.74 | –2.19 (1.99) – 1.51 (0.15) 2.94 (0.44) – – – – |
|                          | $\Psi$(MPX), p(.)                           | 316.61            | 4.30  | 0.10     | 3  | 343.3  | –0.39 (0.15) – 1.51 (0.16) – – – – – |
|                          | $\Psi$(.), p(Ave HP)                       | 318.38            | 6.07  | 0.04     | 3  | 342.42 | –0.71 (0.60) – 1.51 (0.16) – – – 0.18 (0.16) – |
| Pseudacris ocularis      | Naïve estimate§: 0.62                      | 126               |       | 501.7    | 0   | 0.97  | 3  | 544.11 | –1.75 (0.93) – 0.89 (0.11) 3.68 (0.6) – – – – |
|                          | $\Psi$(.), p(Month)                        | 510.2             | 8.41  | 0.01     | 2  | 556.19 | 0.47 (0.40) – 0.88 (0.10) – – – – – |
|                          | $\Psi$(Ave HP), p(.)                       | 511.8             | 10.01 | 0.01     | 3  | 555.13 | –1.19 (0.76) – 0.88 (0.10) – 0.19 (0.17) – – – – |
|                          | $\Psi$(.), p(Month)                        | 512.1             | 10.34 | 0.01     | 3  | 555.49 | 0.47 (0.40) – 0.70 (0.24) – – – – 0.07 (0.06) |
| Gastrophryne carolinensis| Naïve estimate§: 0.73                      | 62                |       | 202.9    | 0.00| 0.93  | 3  | 291.53 | 1.51 (0.70) – 2.55 (0.22) – 0.88 (0.22) – – – – |
|                          | $\Psi$(.), p(Water depth)                   | 209.9             | 7.00  | 0.03     | 3  | 405.53 | 1.14 (0.49) – 1.66 (0.31) – – – – – |
|                          | $\Psi$(.), p(Month)                        | 210.2             | 7.36  | 0.02     | 3  | 406.25 | 1.14 (0.49) – 2.36 (0.37) – – – – – |
Table 2. (Continued)

| Species | Models | No. of detections | QAICc | Δ QAICc* | w† | K‡ | -2 log likelihood | Untransformed coefficients of covariates (standard errors) |
|---------|--------|------------------|-------|----------|-----|-----|-------------------|----------------------------------------------------------|
| Lithobates grillicaudia | Naïve estimate: 0.23 | 13 | 552 | 0 | 96 | 3 | 96.21 | -0.61 (0.57) | -4.11 (0.63) | 1.77 (0.40) | – | – |
| | (γ), (Water depth) | 63.04 | 7.84 | 0.02 | 2 | 11.70 | 3 | 96.21 | -0.99 (0.52) | -2.61 (0.35) | – | – | – |
| | (γ), (Month) | 63.76 | 8.56 | 0.01 | 3 | 113.34 | 4 | 99.57 | 0.99 (0.52) | -3.89 (0.83) | – | – | – |

Covariates: MPX, mean proximity index; amount and distribution of forest cover within 500 m of wetland; water depth, depth of water in each wetland at every sampling occasion; time varying, parameter built into models to account for differences in detection which vary by month, year, or month and year; Ave HP, average hydroperiod of the wetland over the course of the study.

AIC, Akaike Information Criteria.

*Difference in QAICc relative to the top model.
†QAICc weight.
‡Number of parameters in the model.
§Proportion of sampling units where the species was detected.
¶Constant probability of detection.
**Constant probability of occupancy.

Urbanization interfaces with the use of amphibians

Finding that a group of species is sensitive to wetland degradation and also simultaneously sensitive to urban sprawl means that we can use these species as reliable indicators of one type of anthropogenic disturbance. However, it is crucial to note that urban wellfields, the species sensitive to this degradation, are not the only indicators used to monitor the effects of increasing sedimentation and also simultaneously sensitive to urban sprawl. In addition, it seems that urbanization has been shown to contribute to the percentage of the watershed area devoted to olive cultivation (Garcia-Munoz et al. 2010) and thus is less sensitive to the structure of the surrounding habitat.
those with considerably slower larval development could call at the wetland but tadpoles might not survive excessive withdrawal.

To select a reliable set of anuran species to monitor wetland health, we should be aware of their potential responses to a variety of potential stressors, not just the stressor of immediate interest. Critical thresholds in habitat alteration are species specific and related to reproductive potential, dispersal ability, home range size and habitat specificity (e.g. Fahrig 2001). Even within the same taxonomic group or species guild, there is no assurance that habitat changes affecting one species will be the same for other species in the group or guild (Block, Brennan & Gutiérrez 1987). We conclude that while anurans are effective indicators and are complementary to vegetation, the usefulness of this group in monitoring wetland health can be substantially reduced, or eliminated, because they are also simultaneously sensitive to urban sprawl. We urge for careful consideration of confounding factors in any studies examining the utility of indicator species.

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