University of Alberta

The value of stormwater wetlands for supporting multiple life-history stages of the wood frog (*Lithobates sylvaticus*) in the City of Edmonton, Alberta, Canada

by

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I felt the tranquility of
my desert sunrise.
Uplifted by wing beats of a baby bee,
I gained strength to carry on…

I dedicate this thesis to my parents and my dog Guinness

Abstract

I reviewed 32 urban amphibian studies from North America and found most amphibians respond negatively to urbanization (69 negative responses, 6 positive and 35 no effect). Additionally, I conducted amphibian surveys (adult, egg, larvae, and metamorphs) at 75 wetlands located throughout the City of Edmonton, Alberta, Canada, with a focus on the wood frog (*Lithobates sylvaticus*). Wetlands consisted of natural river valley and upland sites, and constructed stormwater wetlands. Breeding male wood frogs occured at 50% of stormwater wetlands versus 93% of natural wetlands. The presence of breeding males was best predicted by the proportion of native vegetation within 100 m of a wetland. Wood frogs successfullly reproduced on stormwater wetlands but relative abundances of eggs, tadpoles and metamorphs were lower than at natural sites. However, stormwater metamorphs were significantly larger which may contribute to higher survivorship and subsequent reproductive success. Stormwater wetlands are required to control flooding and run-off, therefore, future amphibian conservation efforts should focus on preserving native terrestrial habitat surrounding urban wetlands.

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GENERAL INTRODUCTION

Disturbances and alterations of ecosystems by human activity have resulted in extinctions and declines of species worldwide (Pimm et al. 1995). Urbanization is recognized as a major driving force in species' declines globally and throughout North America (Czech et al. 2000, Foley et al. 2005). Amphibians are at the forefront of the global extinction crisis with approximately one-third of all amphibian species listed as threatened (Stuart et al. 2004), of which 80% are likely threatened because of habitat loss (Baillie et al. 2004).

Terrestrial and aquatic habitat loss is common in urban areas, and what habitat remains is usually surrounded by highly homogenized urban features (McKinney 2006). Amphibian species throughout North America and Europe require aquatic habitats to support larval development and terrestrial habitat for their juvenile/adult stage (Smith and Green 2005). Given that many pond-breeding amphibians exhibit strong site fidelity (i.e., philopatry), their populations may be limited by loss of either terrestrial or aquatic habitats.

In North America numerous studies document the relationship between urbanization and amphibian species richness and abundance at landscape scales (Rubbo and Kiesecker 2005, Parris 2006, Gagné and Fahrig 2007). Although it is well established that many North American species respond negatively to urbanization there still is insufficient information on the ecology of amphibians in urban areas for management and conservation (Hamer and McDonnell 2008). To acknowledge the realities and constraints of conservation practice in urban areas, we must first identify what information exists regarding urban amphibian ecology and the general applicability of these data to the conservation and management of urban amphibian populations.

In Canada, the area of urbanized land approximately doubled between 1971 and 1996 (Canadian Biodiversity Information Network 2007). Similarly, the province of Alberta, contains one of Canada's fastest growing urban areas, Edmonton (Statistics Canada 2006). Between 1970 and 1990, 21 to 48% of Alberta's wetlands were lost, largely due to drought and drainage for agriculture (Alberta Environmental Protection 1996). Much of the wetland loss occurred in the aspen parkland; over 60% of the wetlands in the aspen parkland of Alberta have been drained for agriculture and urban development (Alberta Water Resources Commission 1990). Under the *Water for Life Strategy* in Alberta all loss of wetlands is required to be mitigated or compensated, a common but uncertain process in urban landscapes (van der Valk and Pederson 2003). Nonetheless, even though the mitigation of wetland loss is now required, no such policy exists for the maintenance of terrestrial habitat adjacent to wetland sites (Gibbons 2003). The loss of terrestrial habitat surrounding wetlands is especially common in urban landscapes because land is often too expensive and limited for protection of large tracts (Calhoun and deMaynadier 2008). Because human creation and alteration of both aquatic and terrestrial habitats are inevitable in urban settings, increasing our understanding of amphibian use of the resulting urban and isolated native habitats would aid in their conservation.

Stormwater wetlands accompanied by surrounding terrestrial habitat may represent a practical conservation tool for urban amphibians. Thousands of wetlands have been constructed throughout North America, particularly as a means to mitigate wetland loss in urbanized landscapes (Kennedy and Mayer 2002). Although constructed stormwater wetlands may vary in design, the general use of these systems is similar: to prevent flooding, mitigate wetland loss, provide recreation, sequester pollutants and/or provide habitat for various animal species (Smith 2009). Although these wetlands are common and widespread, few studies explicitly examine the success of these wetlands in supporting amphibian communities.

The following two chapters 1) indentify whether studies currently available in the peer-reviewed literature provide us with the knowledge necessary to conserve urban amphibian populations and identify topics in need of greater study and, 2) examine whether stormwater wetlands in Edmonton, Alberta, Canada provide habitat for multiple life-stages of the wood frog (*Lithobates sylvaticus*). I accomplished the first objective by reviewing 32 urban studies from North America to identify the total number of species studied as well as species-specific responses to urbanization. For each study, I summarize the sampling methodologies used to survey amphibians, life-history stages examined, geographic distribution of research, and how each study classifies urban habitat. To achieve my second objective, and fill some of the information gaps identified from objective 1, I conducted surveys to identify which amphibian species occur at urban wetlands throughout the city of Edmonton. Additionally, I examined multiple life-stages of wood frog at 75 wetlands throughout the City of Edmonton. I chose to focus on multiple life-history stages of wood frog because all life stages are essential for a population to persist. For example, if I had only examined occurrence of adult wood frogs, these data may have proved misleading as they would not decipher whether the population was successfully reproducing and recruiting individuals from one life stage to the next. Lastly, I compared frog abundance and densities at multiple life stages between stormwater and natural wetlands to characterize wood frog populations across different urban wetland types.

LITERATURE CITED

Alberta Environmental Protection. 1996. Alberta state of the environment report, aquatic ecosystems. Alberta Government, Edmonton, AB. 153 pp.

Alberta Water Resources Commission. 1990. Wetlands: values and opinions – a draft policy for the management of wetlands in the settled areas of Alberta. Alberta Water Resources Commission, Edmonton, Alberta. 7 pp.

Baillie J.E.M., C. Hilton-Taylor, and S. Stuart. 2004. 2004 IUCN Red List of Threatened Species: A global species assessment. In, p. 217. IUCN, Gland, Switzerland and Cambridge, UK

Calhoun, A. J. K. and P. deMaynadier. (ed.) 2008. Science and conservation of vernal pools in northeastern North America. Taylor and Francis Group. Boca Raton, FL, USA.

Canadian Biodiversity Information Network. 2007. Urban Biodiversity. Online: http://www.cbin.ec.gc.ca/enjeux-issues/urbain-urban.cfm?lang=eng

Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. BioScience **50**:593-601.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science **309**:570-574.

Gagné, S. A. and L. Fahrig. 2007. Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada. Landscape Ecology **22**:205-215.

Gibbons, W. J. 2003. Terrestrial habitat: A vital component for herpetofauna of isolated wetlands. Wetlands **23**:630-635.

Hamer, A. J. and M. J. McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: A review. Biological Conservation **141**:2432-2449.

Kennedy, G., and T. Mayer. 2002. Natural and constructed wetlands in Canada: An overview. Water Quality Resource Journal Canada **37**:295-325.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation **127**:247-260.

Parris, K. M. 2006. Urban amphibian assemblages as metacommunities. Journal of Animal Ecology **75**:757-764.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversty. Science **269**:347-350.

Rubbo, M. J. and J. M. Kiesecker. 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology **19**:504-511.

Smith, B. R. 2009. Re-thinking wastewater landscapes: Combining innovative strategies to address tomorrow's urban wastewater treatment challenges. Water Science and Technology **60**:1465-1473.

Smith, M. A. and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography **28**:110-128.

Statistics Canada 2006. Census snapshot of Canada – Urbanization. In. p. 11. Canadian Social Trends, Catalogue No. 11-008.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science **306**:1783-1786.

van der Valk, A. G. and R. L. Pederson. 2003. The SWANCC decision and its implications for prairie potholes. Wetlands **23**:590-596.

Chapter 2

Do we have the knowledge necessary to conserve urban amphibian populations in North America?

I. INTRODUCTION

Amphibian declines are global in extent and significant attention has been directed towards identifying mechanisms behind declines. Global climate change (Pounds *et al.,* 2006), habitat loss (Stuart *et al.,* 2004), environmental contamination (Bridges & Semlitsch, 2000), disease and pathogens (Lips *et al.,* 2006), as well as overharvesting (Warkentin *et al.,* 2009), all significantly contribute to amphibian extinctions and declines. Particular life histories and habitat requirements make some species of amphibian more susceptible to environmental changes than others (Sodhi *et al.,* 2008). Reminiscent of Neotropical migrant songbird populations that declined because of loss of over-wintering habitats in Central and South America while breeding habitat in North America remained unaltered (Robbins *et al.,* 1989), many amphibian species display life histories that straddle both aquatic and terrestrial environments and populations can decline due to degradation of either habitat. Habitat loss is likely the most significant contributor to amphibian declines globally (Bickford *et al.,* 2008) and a pervasive force in habitat loss is urbanization (McKinney, 2002; McKinney, 2006).

Amphibian species in North America are the most studied globally (Brito, 2008), yet very little is known regarding species-specific responses to habitat loss caused by urbanization. The negative impacts of urbanization on amphibian richness and abundance have been studied for some North American species (Rubbo & Kiesecker, 2005; Parris, 2006; Gagné & Fahrig, 2007), yet other studies suggest that some wetland breeding amphibian species exhibit resilience to the impacts of urbanization (Rubbo & Kiesecker, 2005; Windmiller & Calhoun, 2008). Ambiguities exist because most studies to date only document negative associations between urbanization and amphibians and do not definitively identify mechanisms that link predictive urban metrics and response variables such as abundance or species richness (Hamer & McDonnell, 2008). More importantly, studies of urban amphibian ecology are relatively uncommon (Windmiller & Calhoun, 2008; Mitchell *et al.,* 2008) and recent literature (Hamer & McDonnell, 2008; Mitchell *et al.,* 2008) does not fully address the lack of information regarding several key areas of amphibian ecology such as terrestrial habitat availability, habitat use and selection, species-specific responses to urbanization, and amphibian movements and dispersal in urban landscapes. Such gaps in our knowledge impair our capacity to devise conservation strategies to reverse or prevent declines (Brito, 2008).

A major challenge for conservation is the occurrence of human settlement in areas of high biodiversity (Burgess *et al.,* 2007). Land prices typically rise with increased human population density and make conservation an expensive exercise near human settlements (Luck *et al.,* 2004). To acknowledge explicitly the realities and constraints of conservation practice in urban areas where land is expensive and limited, we must first identify what information exists regarding urban amphibian ecology and the general applicability of these data to the conservation and management of urban populations in North America.

Herein, I quantify the number of amphibian species studied in urban settings, characterize species specific responses to urbanization, and assess whether suitable attention has been given to North American species under threat by urbanization (threat as defined by IUCN [2008]). Because particular behaviors, such as movement capabilities, which are governed by body size, make a species more or less susceptible to disturbances (Semlitsch, 2008), I investigate whether species that move longer distances respond more negatively to urbanization than species with more limited movement capabilities. Additionally, I ask a range of questions that I believe essential to urban conservation, yet may be unanswered by the current literature: 1) Are urban studies conducted in geographic locations of high amphibian richness and endemism?, 2) Do urban studies consider species "at risk"?, 3) Do specific genera and/or amphibian life-history stages receive more attention in urban literature as a result of survey and sampling methods?, 4) Do studies define "urban" in ways that allow for comparisons among studies?, and lastly, 5) Are the current scales or spatial extents used in analysis applicable to conservation in urban landscapes?

II. METHODS: COLLATING DATA FROM URBAN AMPHIBIAN STUDIES

I use the peer-reviewed literature to examine common themes that emerge from North American urban studies. I used two primary sources to find articles on urban amphibian ecology: Hamer & McDonnell (2008) and Mitchell *et al.* (2008). All studies were constrained to North America and published no earlier than 1990. I reviewed 20 primary scientific literature sources on urban amphibian ecology from Table 1 in Hamer & McDonnell (2008). From Mitchell *et al.* (2008) I reviewed six empirical studies from Sections I – IV.

I performed an additional search for articles on *Web of Science* using the terms (amphibian* AND urban*) that yielded 121 studies, of which three were included in my review as they explicitly examined urban amphibian ecology. Three additional studies that were cited by studies reviewed in Hamer & McDonald (2008) were included in my review. In total, I reviewed 32 studies (Table 2.1): 20 from Hamer & McDonnell (2008), six from Mitchell *et al.* (2008), three from my ISI search, and three cited in literature reviewed by Hamer & McDonnell (2008).

(1) Human population and amphibians across North America

I examined the spatial congruence between human population and amphibians in North America in a Geographical Information System (Fig. 2.1; see Luck *et al.,* 2004). I also examined broad correlative relationships between human population size and 1) species richness, 2) species endemism, and 3) number of species "at risk" according to IUCN (2004). All geospatial data were collected for 110 terrestrial ecoregions across North America (Olson *et al.,* 2001, also see Ricketts *et al.,* 1999 for data acquisition information). I used WildFinder (ver. 01.06) from the World Wildlife Fund to acquire all data regarding species distributions and conservation status. Species considered "at risk" were those listed as critically endangered (CR), endangered (EN), vulnerable (VU), and near threatened (NT). I included NT amphibian species in order to represent all species suspected by IUCN to be in decline. Human population counts for 1990 and 2000 were obtained from the Gridded Population of the World, Version 3 http://sedac.ciesin.columbia.edu/gpw/global.jsp). Years 1990 and 2000 were chosen based on available data. Multiple polygons existed for each ecoregion, therefore, I had a total of 2597 polygons that were included in my analysis. Additionally, because grid cells and ecoregions are continuous, the likelihood for spatial autocorrelation is high; therefore, I do not report *P*-values for my analyses (Luck *et al.,* 2004). Instead, I recorded the correlation coefficients (which are unaffected by spatial autocorrelation) to represent the relationship between variables (Luck *et al.,* 2004). All data were either log10 or power $(X + 10)^P$ transformed to achieve normality. However, because of a large number of zeros, the data were heavily skewed following the best normalization; I therefore, used non-parametric Spearman rank correlations (Luck *et al.,* 2004).

(2) Species-specific responses to urbanization

I assessed the degree and strength of the response by each species to urbanization and assigned one of the following four responses for each species in each study: negative, positive, neutral, and unknown (no assessment offered). Each response was defined by the following parameters: abundance, species occurrence (presence or absence), mortality, and/or recruitment. Therefore, a negative response, for example, can be characterized by having higher abundances, greater occurrence, higher species richness, lower mortality, and greater recruitment at non-urban over urban sites. I relied on the authors of each study to assess responses. For example, Rubbo and Keisecker (2005) provide an example of a negative response to urbanization by three amphibian species. They state "this decrease in richness was attributable to a decrease in occurrence of wood frogs (*Rana sylvatica*) and ambystomatid salamanders (*Ambystoma maculatum* and *A. jeffersonianum*) in urban sites". An example of a positive response to urban is as follows "Three species of ranids, *Rana utricularia*, *R. grylio*, and *R. catesbeiana*, were found in higher abundances at the residential development than at the park" (Delis *et al.* 1996). Lastly, Riley et al. (2005) provide an example of a neutral response by stating "At the stream scale, larval treefrog density was not related to urbanization in 2000…, although in 2001 larval density was marginally higher in urban streams (1.21 tadpoles/m vs. 0.82

tadpoles/m in natural streams”. Because *Hyla regilla* exhibited a largely neutral response as well as a slightly positive response to urbanization, I characterized this as an overall neutral response. Additionally, the authors state “For Pacific treefrogs (*Hyla regilla*)…direct urbanization effects were not found”. Fourteen studies contained only ambiguous reporting; therefore, I devised a survey that was sent to each author of these studies to provide species-specific assessments. Five authors replied with feedback, two replied but were unwilling to provide feedback, and seven did not respond. For the remaining nine of 14 studies, where possible, I evaluated species’ responses based on figures and tables that distinctively indicated specific responses to urbanization. All species-specific responses were tallied and descriptive statistics were used to display differences in responses to urbanization across all amphibians studied. In order to determine whether the most threatened North American species have received attention in the literature, I recorded all species identified as under threat by urbanization by IUCN (2008). Criteria for species “at risk” followed the same criteria as my classification of Wildfinder data (“at risk” = CR, EN, VU, and NT).

(3) Movement and species-specific responses to urbanization

Biphasic lifestyles mean that movements (both migration and dispersal) to and from both aquatic and terrestrial habitats are essential to the success of most North American amphibian species (Semlitsch, 2008). Movement therefore is important to consider for successful conservation of amphibians. I examined whether an association existed between a species’ response to urbanization based on my review and its maximum recorded movement distance. A response index was derived for each species by measuring the proportion of studies that report negative responses to urbanization. To determine this index, I divided the number of studies with negative responses to urbanization by the total number of studies that reported a response (i.e., negative + positive + neutral responses) to urbanization. Studies that failed to report a response ("unknown") were not included in the total. Only species with three or more responses documented in the literature were included in my analysis. Additionally, I recorded the maximum movement distance from several sources: Amphibia Web (2009), Smith & Green (2005), Semlitsch (1998), and Calhoun & deMaynadier (2008). If a maximum distance was not found, I searched ("species"* AND [movement* OR migration* OR dispersal*]) in ISI to find primary literature presenting distance values. Adult migration distances were recorded for all but two species (*Hyla versicolor* and *H. chrysoscelis*) and I thus used metamorph migration distances for these frogs. All data were normally distributed and I used simple linear regressions to assess the relationship between response indices and maximum movement distances. I used Cook's distance to determine if any outlier point exhibited a large degree of influence on the regression ($C_i > 1$). Cook's distance values indicated that *Rana catesbiana* exhibited a large degree of influence on the regression (C_i=1.612), and therefore this species was considered a significant outlier. Additionally, I excluded *R. catesbiana* because it was exotic to the study area in three studies. All statistical analyses were conducted in SPSS v. 17.0 (SPSS Inc., Chicago, IL, 2008) and SigmaPlot v. 11.0 (SYSTAT Inc., Chicago, IL, 2008).

(4) What has been studied in urban amphibian ecology?

I summarized the following factors for each of 32 studies: 1) taxonomic group (i.e., anuran or caudata) studied, 2) breeding habitats for each species, 3) sampling methods used, 4) life-history stages (e.g., adult, juvenile, young of year, tadpole, egg) considered, 5) whether a study considered reproductive recruitment (defined by the presence of young of year) as a response variable, 6) whether movements of individuals were recorded, 7) whether a habitat gradient of natural vegetation (e.g., forest to agriculture to urban) was involved, 8) minimum and maximum extent of examination, and 9) number of land cover types classified as urban.

(5) Taxonomic groups studied and sampling methods

In order to determine which proportion of North American amphibians were studied in urban literature, I recorded all anuran and caudata species in North America recognized by Crother (2000) and all species studied within the 32 urban studies. The only exception was the *Ambystoma laterale-jeffersonianum* complex where I treated *A. jeffersonianum*, *A. laterale*, and *A. laterale-jeffersonianum* as separate taxonomic units. A taxonomic attention index (AI_{taxon}) was calculated for Anura and Caudata. This index was generated by dividing the number of papers on each Order in North America by the number of species in the Order in North America (Brito, 2008). I characterized the breeding habitats for each species studied in urban settings to determine if amphibians from a particular breeding habitat were understudied. Breeding habitats were identified using AmphibiaWeb (2009). I grouped bog, swamp, temporary pools, ditches, wetlands, ponds, and lakes as “wetlands/temporary pools”, and springs, creeks, seeps, and streams as “streams/springs”. If amphibians were said to breed in both wetland and stream habitats, I categorized them as “wetland/stream” breeders. Other breeding habitats included “terrestrial”, “wetland/terrestrial”, “cave” and “unknown”. Furthermore, because sampling techniques increase or decrease detectability of specific groups of amphibians (e.g., call surveys only record anurans), I documented sampling protocols for each reviewed study. These methodologies include breeding call surveys, egg mass surveys, visual surveys, aquatic dipnets, drift fence/funnel traps, pipe sampling, and minnow traps.

(6) Life-history stages and scale

I quantified all life-history stages used in analyses for each study and whether these studies considered recruitment. Studies that examine reproductive recruitment must have considered the metamorphic life-history stage (i.e., young-of-year) in analyses. Studies that did not specifically examine the metamorph class, but instead grouped metamorphs with adults and juveniles as a sign of species’ presence and absence did not meet the criteria of “recruitment”. Additionally, studies that examined movements were noted.

All minimum and maximum scales (i.e., minimum and maximum extents) used for landscape examinations were recorded from each study. For example, if a study examined a species occurrence at wetlands in relation to surrounding urban land cover at 0-100, 0-200, 0-300, 0-400, and 0-500; the minimum scale used is 100 m and the maximum scale used is 500 m. I defined a gradient study as one that compared response variables between two or more habitat types (e.g., native habitat, agriculture, or urban). Additionally, I examined the variation in urban classification schemes among studies, and how these studies defined their urban metrics (e.g., residential, commercial, and industrial combined into a single urban metric). I then summarized all results using descriptive statistics in tables, and figures to iterate trends visually.

III. RESULTS

Human population counts were strongly correlated with amphibian species richness, and the number of “at risk” species across ecoregions (Fig. 2a, b). Similarly, population growth (1990 – 2000) was also highly correlated with species richness (r_s = 0.740, n = 2597). Ecoregions with high species endemism were correlated with areas of high human populations (r_s = 0.334, n = 2597; Fig. 2.1). More than half of the 32 reviewed studies occurred in moderately species rich areas in the Midwest (seven) and Northeastern (nine) part of USA, with five studies occurring in the Southeast, an area with the highest amphibian diversity and endemism in North America (Fig. 2.1). Additionally, six studies occurred in western North America (three in Southwest and three in Northwest) and five in central Canada (i.e., Québec and Ontario; Fig. 2.1).

Urban studies examined 38 anuran and 24 caudate species, and represented approximately 40% of North American anuran species and 14% of caudate species. The AI_{taxon} for Anura and Caudata was 0.263 and 0.127, respectively, which suggests that anurans received more attention in urban studies than caudates. The three most species rich Caudata genera in North America (*Plethodon*, *Eurycea*, and *Desmognathus*) were most understudied (4 species investigated in urban literature (U) / 53 total in North America (NA) species for *Plethodon*, 3 U / 22 NA *Eurycea*, and 2 U / 17 NA *Desmognathus*; Fig. 2.3). Conversely, the four largest anuran genera were most studied

(12 U / 26 NA *Rana*, 8 U / 19 NA *Bufo*, 7 U / 13 NA *Psuedacris*, and 8 U / 10 NA *Hyla*; Fig. 2.3).

Of the 32 urban studies, relatively few were at the population-level, rather 19 of the 32 were at the community-level thus few species-specific responses were recorded (Table 2.1). My review of literature uncovered 193 responses (negative, positive, neutral, or unknown) to urbanization (144 for Anura and 49 for Caudata), from 62 species (Table 2.2). The number of negative responses outnumbered the number of positive responses by a factor of 12; 36% (69/193) were negative compared to 3% (6/193) positive and 18% (35/193) neutral. The majority of responses, i.e., 43% (83/193), however, were unknown (Table 2.2). Of the 32 North American amphibians threatened by urbanization according to IUCN, only six were represented by studies in the urban literature and only three responses (1 positive, 1 negative, and 1 neutral) were recorded. My analyses indicated a significant negative association between maximum movement distances and responses to urbanization based on 11 amphibian species ($R^2 = 0.499$, $P = 0.015$). More specifically, a higher proportion of responses were negative for species with greater movement distances than smaller movement distances (Fig. 2.4).

Amphibians that breed in wetlands and wetlands or streams have received the most attention in urban environments. Wetland or stream breeders are one of the least species-rich breeding guilds for caudates, but the most species-rich anuran guild (Table 2.3). Terrestrial breeding salamanders are the most species-rich guild of caudates in North America, yet only 6% of terrestrial breeding salamander species were studied. Similarly, the second most species-rich caudate guild, stream breeders, were understudied with only 12% of species included in urban research.

Seventy-eight percent of response metrics (e.g., presence/absence) for urban studies were assessed based on adults (25/32 studies), 50% on larvae (16/32 studies), and/or 38% on egg masses (12/32 studies). Only two studies include the juvenile stage (9%) and three studies the metamorphic stage (6%). One additional study sampled tadpoles in late Gosner (i.e., development) stages (≥ stage 25) as an indicator of metamorphosing individuals. Of the five studies that considered the metamorphic life-history stage, only three studies consider recruitment in their analyses. Call surveys (*N* = 13), visual surveys (*N* = 13), dipnet sampling (*N* = 11), and egg mass surveys (*N* = 9) were the most commonly used survey technique. Very few studies used more intensive sampling methods such as drift fences and pitfall traps (*N* = 4), funnel traps (*N*= 6), or pipe traps (*N* = 1). Only three of 32 studies examined amphibian movements. Two of these were case studies in Mitchell *et al.* (2008) and examined movements via drift fences; the third used fluorescent-powder tracking (Birchfield & Deters, 2005).

According to Wiens (1989), scale has two components, extent and grain. Extent is the spatial area defined as the landscape, and grain (or resolution) is the smallest area for which the study records values or characteristics. Extent of study was primarily based on dispersal and migration distances of greater than 500 m. The average smallest analytical extent for urban studies was 497 ± 491 m SD (*N* = 22; range: 5 – 1500 m, median = 400 m, mode = 500 m) and the average maximum analytical extent was 2360 ± 2860 m SD (*N* = 21; range: 10 – 10000 m, median = 1000 m, mode = 1000 m).

None of the 32 studies explicitly examined microhabitat selection (e.g., amphibians selecting habitat based on variables such as leaf litter and soil moisture); however, 10 urban studies compared their response metric against an independent variable at local habitat scales, all within 50 m of pond's edge. The majority of studies (*N* = 19) examined response variables across a forest to agriculture to urban gradient, while 11 studies were conducted across a forest to urban landscape and one study compared agriculture and urban sites, and one study forest and golf course. Over half of the studies (14 of 24) combined multiple urban land-uses into single urban metrics (and five did not define "urban" in their study.

IV. DISCUSSION

(1) Urban amphibians in North America

Despite the fact that on a global scale, amphibians are best studied in North America (Brito, 2008), North American studies fail to examine the effects of urbanization equally across amphibian genera and breeding guilds. As is true with amphibian conservation studies in general, urban research is skewed towards community-level analyses and focuses heavily on wetland-breeding amphibians, many of which display conflicting responses to urbanization (Brito, 2008). Numerous species with small and large ranges occur in densely populated areas in North America (Luck *et al.,* 2004). At the ecoregion-level, I found a positive relationship between amphibian richness, endemism (i.e., endemic to a particular ecoregion), and occurrence of species "at risk" with high human population. It is therefore imperative that more studies occur in these conflict areas with high diversity, endemism and human population density such as the Appalachian Mountains and ecoregions along the western coast of North America (e.g., cascade mixed forest and California coastal range). When species-specific information was examined, a large number of species, including those under the most threat from urbanization according to IUCN, either lacked information in the context of urban environments or provided conflicting responses. Nonetheless, my data suggest that overall, North American amphibians respond negatively to urbanization.

(2) Limitations in urban amphibian ecology

Contrary to Hamer & McDonnell (2008), I found that few North American studies examine movement (e.g., dispersal) in urban and suburban areas. To date, no urban studies have examined microhabitat use by amphibians, only three have studied movement patterns, and few studies examined particular natural and life history traits characteristic of organisms in urban landscapes (but see Mitchell *et al.,* 2008). Finding data-deficient areas in any field of study is likely not challenging, as every field has its limitations, however, I believe urban amphibian ecology is limited in four basic areas (species-specific responses, movement patterns, microhabitat use, and the study of various life history stages) that are paramount for science-based conservation, particularly for space-deficient urban landscapes. I provide three examples from my review to illustrate the limits of our knowledge:

1) According to my analysis, North American species as a whole respond negatively to urbanization. One potential mechanism behind this relationship is a species' movement capabilities. A widely held notion is that populations with the best dispersal ability are most resistant to habitat fragmentation and loss (Kareiva & Wennergren, 1995; McCarthy, Lindenmayer & Drechsler, 1997); however, I found that highly vagile species were more likely to respond negatively to urban disturbances. These trends are similar to the findings of Gibbs (1998) who

reported that a sedentary species, the redback salamander (*Plethodon cinereus*), was resilient to fragmentation while a widely dispersing species, the red-spotted newt (*Notophthalmus viridescens*), was less resistant. Why certain amphibian species respond differently to fragmentation remains largely uncertain as few studies examine whether amphibians can effectively move through urban landscapes. If species with the capability of moving greater distances are more susceptible to urbanization than less motile species, how then do we manage species that require large patches of habitat in urban landscapes with little "unused" land?

2) Of the 65 species investigated in my reviewed literature, approximately 64% showed a positive response, no response, or responses to urbanization were not reported. Moreover, these responses were correlative, as most studies primarily examined relationships between response variables (e.g., abundance and/or species richness) and urban metrics (e.g., % residential, commercial, and/or industrial) at the landscape scale. Why, out of four studies that reported specific responses for chorus frog (*Psuedacris triseriata*), were two "negative", one "positive", and one "neutral?" I provide a few possible explanations: i) these discrepancies in a species' responses to urbanization are explained by geographic context, ii) the degree and severity of urbanization was defined differently in each study, iii) the duration of urbanization varied across studies, or iv) responses were defined and/or measured differently across studies. I cannot definitively answer this question; however, I suggest two ways for increasing comparability among future studies.

First, researchers should examine specific behaviors, such as movement patterns, as well as traits related to life history stages (e.g., drought tolerance based on body size) that make species more or less susceptible to urban disturbances. Second, research should document which urban landscape metrics (e.g., residential or commercial structures, remnant patches of native vegetation) hamper or promote the persistence of amphibian populations. Until researchers focus on metrics, such as local habitat availability and suitability in urban landscapes, it will be impossible to know whether amphibians perceive differences between a natural landscape, consisting of rocks, woody debris, and seeps, and an urban landscape with decorative stone, wood chip mulch, and sprinkler systems.

3) Several recent non-urban studies investigated the relationship between landscape structure and amphibian dispersal and found that forest-dependent amphibians avoid crossing open fields, pastures, clearcuts and roads, and in turn orient towards forests and away from open fields (Marsh *et al.,* 2004; Rothermel 2004; Rothermel & Semlitsch 2002). Urban sites resemble open-canopy natural vegetation (Birchfield & Deters 2005; Paton, McDonough & Montieth, 2008). The avoidance of open-canopy habitats by forest-dependent amphibians, therefore, is likely a response to changes in the distribution of suitable microhabitats that act as refugia for avoiding desiccation and/or predators (Baughman & Todd 2007). However, this explanation is speculative because microhabitat and movements in urban landscapes have rarely been examined (exceptions are Paton, McDonough & Montieth, 2008; Husté, Clobert & Miaud,

2006 and Birchfield & Deters 2005, all of which examine landscapes that are not highly developed such as urban parks and golf courses). Recent studies suggest that areas with short grass do not act as dispersal barriers (Paton, McDonough & Montieth, 2008), but that some species of frog (i.e. green frog (*Rana clamitans melanota*)) may preferentially direct movements towards these habitats as they offer less resistance (Birchfield & Deters 2005). Although these preferences may be a response to higher than average precipitation (Birchfield & Deters 2005) and the above scenario may vary by species and geographic location, such studies call to question whether the avoidance of open-canopy habitats reported by non-urban studies are applicable to amphibian management in all urban landscapes. Moreover, conservation practitioners should use caution when applying information derived from native habitats in management plans of urban landscapes or results from studies conducted in forested ecosystems to cities located in regions dominated by grassland, shrubland or desert.

(3) Amphibian groups considered in urban amphibian ecology

My review showed that anuran amphibians are more studied in urban environments in North America than caudate species, particularly species that are wetland-breeding obligates or that opportunistically breed in both wetlands and streams. In contrast, Brito (2008) found that caudate species were the most studied group of amphibians in terms of conservation issues. The bias towards anuran species in urban studies is likely reflective of correlative studies that use call survey techniques as a means to survey rapidly and easily a large number of urban habitats at a landscape scale. Many salamander species, particularly terrestrial breeding salamanders in the genera *Plethodon* and *Eurycea*, are highly cryptic organisms which makes sampling intensive and difficult (Davis, 1997). This relationship is apparent from my data, which shows that terrestrial breeding salamanders, though the most species-rich, are the most understudied North American amphibian in urban environments. The Southeastern USA contains the highest caudate diversity in the world (Petranka, 1998), with many endemic species, some of which have been very recently described for the first time (Camp *et al.,* 2009), yet few urban studies have occurred in this region. The Southeast has also recently experienced the most significant losses of habitat to urban development in North America (Fulton *et al.,* 2001) and high population growth, and thus I strongly suggest future research focus on cities there.

(4) Life-history stages considered in urban amphibian ecology

Another key area in need of greater understanding and research is the effect of urbanization on the reproductive success of amphibians, as well as the survival of individuals at varying life history stages. Studies that sampled amphibians in urban wetland sites conducted breeding call surveys (Gagné & Fahrig, 2007), larval sampling (Rubbo & Kiesecker, 2005), visual and auditory surveys (Houlahan & Findlay, 2003), and egg mass surveys (Skidds *et al.,* 2007; Egan and Paton, 2008). These results did not reflect the success of offspring recruiting into subsequent age classes and life-history states. I found that: 1) few studies monitored amphibians of all life-history stages through the entire sampling season and 2) very few urban studies sampled for metamorphs. Additionally, stage-specific response patterns to urbanization are not understood; 50% of the reviewed studies combined multiple stages into one measure of species occurrence. Monitoring of all age-classes is critically important because individuals of different age classes are behaviorally unique and have specific habitat requirements. They therefore respond differently to disturbances (Rothermel & Semlitsch, 2002; Rothermel, 2004; Lowe, 2005). Hence, management of a species based on data from a single age class may be counter-productive (Rothermel & Semlitsch, 2002). For example, newly constructed urban wetlands may intercept amphibians as they disperse, yet data based on adult and/or juvenile presence does not adequately reflect population persistence through time. The presence of young of year, however, suggests that the population present is reproducing and likely not just maintained by immigration. More continuous sampling of all life-history stages throughout the entire sampling season, that includes mark-recapture analysis via drift fence and pitfall trapping (Trenham & Cook, 2008; Windmiller *et al.,* 2008), would provide useful data regarding urban amphibian behavior, direction of movements, recruitment, and population responses to urbanization. Furthermore, future urban studies should incorporate breeding success (i.e., the presence of metamorphs) as a response variable (as done in Windmiller *et al.,* 2008).

(5) Scale in urban amphibian ecology

To date, there is consistency, but not variety, in scale among urban studies as many studies are biased towards landscape-level investigations. Few urban studies are conducted at local scales with sample sites that immediately surround breeding habitats. It is recommended that management issues be addressed at both local population and metapopulation scales (Semlitsch, 2008). Land that exists in urban areas is often expensive making direct acquisition improbable for most conservation efforts (Baldwin & deMaynadier, 2009). Thus, the results presented from urban studies that only used landscape scales are not entirely applicable for identifying the minimum amount of habitat needed to maintain amphibian populations in urban landscapes. Based on the mean radius (1432 m) of the 19 studies summarized by Hamer & McDonnell (2008) and a suggested 10 km dispersal zone for some amphibian species (Smith & Green, 2005), a management plan that incorporated these extents would require an area of approximately 644 ha and 31,416 ha surrounding a wetland, respectively. Are such areas realistic in an urbanized landscape? Even if spatially explicit models were to reduce required land by 2/3 as suggested in Baldwin, Calhoun, & deMaynadier (2006), a spatially explicit management plan would still require areas of 215 to 10,472 ha surrounding each breeding wetland. Perhaps large scale examinations are appropriate prior to urban development because pre-development management plans have the flexibility to incorporate landscape connectivity (e.g., via corridors and/or reserves) to maintain amphibian populations. In *post-hoc* management schemes, however, large-scale analyses have little applicability because undeveloped space in a pre-existing urban landscape is too limited and expensive.

(6) Urban classification in urban amphibian ecology

Previous reviews suggest that gradient studies moving from native habitat to rural to urban areas are needed (Hamer & McDonald, 2008); however, my data suggest that, at least in North America, the majority of urban studies actually occur across urban to rural to native habitat gradients. Placing behavior, ecology, and scale aside, I believe another major constraint in urban amphibian ecology studies in North America is not the context of study area or examination across habitat types, but instead the inconsistency among studies in defining urban landscape metrics. A majority of studies in my review combined multiple urban land classes into one urban metric. Urbanized land has been classified in previous studies as developed land (Price *et al.,* 2006), area covered by sealed roads (Parris, 2006), percent of built-up land (Hodgkison, Hero & Warnken, 2007), and area of residential development as defined by number of buildings (i.e., houses, barns, and commercial structures; Skidds *et al.,* 2007). Gagné & Fahrig (2007) group residential, commercial, and industrial development together as urbanized land, whereas Rubbo & Kiesecker (2005) classify urbanized land by population density. By grouping residential, commercial, and industrial land, Gagné & Fahrig (2007) likely oversimplify the differences between these complex land-use classes. Grouped land categories may be deceiving as commercial and industrial landscapes contain more impermeable surfaces, while residential landscapes often contain patches of vegetation that potentially offer microhabitats for more amphibians. Rubbo & Kiesecker (2005) categorize urban, suburban, and rural areas by population densities, resulting in a similar oversimplification. Analyses based on human population densities disregard areas of considerable development with low population densities, such as industrial and commercial sites. Assumptions and generalizations regarding urban landscapes should be avoided, as grouping urban land classes likely masks the differences between habitat types and may lead to uninformed and misguided land management decisions. Additionally, the field of urban amphibian ecology would benefit from research that assesses how a single response variable correlates with multiple urban land classifications (as done in Clark et al. 2008).

(7) Major considerations for on the ground conservation and management

Among the various causes for global amphibian decline, human-caused habitat loss remains the most influential. No single conservation strategy surpasses the need for habitat preservation, however, considering the realities and constraints of conservation practice in urban areas, I make the following recommendations for future studies that can help address on-the-ground conservation and management:

1) **Focus on areas supporting high species richness*:*** More research is needed on species-rich areas, such as the Southeast USA, on endemic species, and on species "at risk". Past urban literature has been focused on landscape-level examinations, particularly on non-endemic and secure wetland breeding species, thus little is known of current conditions in many species-rich areas.
2) **Regional conservation strategies are imperative for maintaining biodiversity*:*** We need to start considering species that are still wide-spread, but are regionally declining. Species that are common now can easily decline or become extirpated without proactive management. For example, *R. sylvatica*, though common throughout Northeastern North America, is now extirpated from many parts of the Midwest. Regional conservation strategies can and should incorporate species that are suffering local declines because of urbanization and thus it is imperative **to** have conservation strategies in place before species begin to decline.

3) **Species-specific responses are essential to management**: My review showed that many species responses to urbanization are either unknown or ambiguous (i.e., species that exhibit mixed responses). Therefore, studies should assess species-specific responses to urbanization to allow for effective population-level management (Cushman, 2006).
4) **Urban amphibian movements must be considered**: Understanding amphibian movements is critical to many aspects of conservation (Semlitsch, 2008) yet few studies examine movements in urban environments. More data on amphibian movements may result not only in population-level management, but may also lend insight into key terrestrial features that maintain connectivity, thus increasing the potential for long-term regional persistence of species in urban environments (Semlitsch & Rothermel, 2003).
5) **Smaller scale examination:** Most urban studies in North America occur at extents of 1000 m or greater. Contrary to other recommendations (e.g., those offered in Hamer & McDonnell, 2008) that advocate larger scale studies, I encourage smaller scale examinations of local habitat selection and use, which will allow for both feasible and practical conservation practice in highly urbanized environments. It is impractical to advocate large scale conservation "*a posteriori*" in highly developed environments.
6) **Consideration of entire life cycle**: To date, most urban studies use the adult life-history stage as the source of response metric for analyses, which may lead to misinformed management decisions. I advocate the analysis of multiple response variables (including multiple life-history stages) in future

studies and encourage the pairing of life-history stages with appropriate habitats. For example, analyses that compare larval and metamorph data to aquatic habitat parameters and adult/juvenile data to terrestrial habitat parameters should be considered.

7) **Additional information to improve conservation:** Behavioral and ecological data can be used to examine the optimum size and composition of habitat patches in urban areas necessary for maintaining, not just generalist species, but also specialist species that are more sensitive to habitat disturbances (Cook, 2008). Conservation of single populations relies on accurate estimates of the size of core terrestrial habitat that promotes persistence of populations (Semlitsch, 2008); however, such requirements may significantly vary from species to species and from population to population. Therefore, planners need distinct guidelines if biogeographical concepts are to be incorporated in urban planning (Windmiller *et al.,* 2008; Westmacott, 1991). Furthermore, acquiring general knowledge of local amphibian demography and habitat use through studies that are performed pre- and post-urbanization, would further aid in regionally appropriate management plans (see Windmiller *et al.,* 2008 for further recommendations on design of pre- versus post-urbanization case studies of amphibian populations).

V. CONCLUSION

My review highlights that, overall, many North American amphibians respond negatively to urbanization; however, more information is required (e.g., regional species-specific responses to urbanization) before conservation practitioners have the necessary information needed to solve regional conservation problems effectively (Gilioli *et al.,* 2008; Schmidt, 2008). Models that consider the many constraints that exist in real life conservation practice are needed (e.g., limited space in urban environments), as such constraints make many solutions impossible (Schmidt, 2008). In urban landscapes, considerable attention must be given to determining a scale of study that guides both feasible and practical conservation and management. Interfacing urban metrics with the complex life cycle of amphibians by including multiple life-history stages will likely yield more robust information regarding the negative impacts of urban development on amphibian populations. Furthermore, information regarding amphibian movements and habitat preferences, coupled with appropriate scales and land classifications, should allow for spatially explicit land management plans that may protect urban amphibian populations through time.

I. REFERENCES

AMPHIBIAWEB: Information on amphibian biology and conservation. [web application]. 2009. Berkeley, California: AmphibiaWeb. Available: http://amphibiaweb.org/. (Accessed: 3.3.09).

BALDWIN, R. F., CALHOUN, A. J. K. & DEMAYNADIER, P. G. (2006). Conservation planning for amphibian species with complex habitat requirements: A case study using movements and habitat selection of the Wood Frog *Rana sylvatica*. *Journal of Herpetology* **40,** 442-453.

BALDWIN, R. F. & DEMAYNADIER, P. G. (2009). Assessing threats to pool-breeding amphibian habitat in an urbanizing landscape. *Biological Conservation* **142,** 1628-1638.

BARRETT, K. & GUYER, C. (2008). Differential responses of amphibians and reptiles in riparian and stream habitats to land use disturbances in western Georgia, USA. *Biological Conservation* **141,** 2290-2300.

BAUGHMAN, B. & TODD, B. D. (2007). Role of substrate cues in habitat selection by recently metamorphosed *Bufo terrestris* and *Scaphiopus holbrookii*. *Journal of Herpetology* **41,** 154-157.

BICKFORD, D., SODHI, N.S., DIESMOS, A.C., LEE, T.M., KOH, L.P., BROOK, B.W., SEKERCIOGLU, C.H., & BRADSHAW, C.J.A. (2008). Forgetting Habitat Loss in Amphibian Extinctions – Missing the Forest for the Disease**.** A response to: Riding the Wave: Reconciling the Roles of Disease and Climate Change in Amphibian Declines Lips K.R., Diffendorfer J., Mendelson III J.R., Sears M.W. *PLoS Biology*, doi:10.1371/journal.pbio.0060072.

BIRCHFIELD, G. L. & DETERS, J. E. (2005). Movement paths of displaced Northern Green Frogs (*Rana clamitans melanota*). *Southeastern Naturalist* **4,** 63-76.

BOWLES, B. D., SANDERS, M. S. & HANSEN, R. S. (2006). Ecology of the Jollyville Plateau salamander (*Eurycea tonkawae* : Plethodontidae) with an assessment of the potential effects of urbanization. *Hydrobiologia* **553,** 111-120.

BRIDGES, C. M. & SEMLITSCH, R. D. (2000). Variation in pesticide tolerance of tadpoles among and within species of ranidae and patterns of amphibian decline. *Conservation Biology* **14,** 1490-1499.

BRITO, D. (2008). Amphibian conservation: Are we on the right track? *Biological Conservation* **141,** 2912-2917.

BUNNELL, J. F. & ZAMPELLA, R. A. (1999). Acid water anuran pond communities along a regional forest to agro-urban ecotone. *Copeia***, 1999,** 614-627.

BURGESS, N. D., BALMFORD, A., CORDEIRO, N. J., FJELDSA, J., KUPER, W., RAHBEK, C., SANDERSON, E. W., SCHARLEMANN, J. P. W., SOMMER, J. H. & WILLIAMS, P. H. (2007). Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation* **134,** 164-177.

CALHOUN, A.J.K., & DEMAYNADIER, P.G. (2008). Science and conservation of vernal pools in northeastern North America. CRC Press, Boca Rotan.

CAMP, C. D., PETERMAN, W. E., MILANOVICH, J. R., LAMB, T., MAERZ, J. C. & WAKE, D. B. (2009). A new genus and species of lungless salamander (family Plethodontidae) from the Appalachian highlands of the south-eastern United States. *Journal of Zoology* **279,** 86-94.

CARR, L. W. & FAHRIG, L. (2001). Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* **15,** 1071-1078.

CLARK, P.J., REED, J.M., TAVERNIA, B.G., WINDMILLER, B.S., & REGOSIN, J.V. (2008). Urbanization effects on spotted salamander and wood frog presence and abundance. In: *Urban Herpetology* (eds MITCHELL, J.C., JUNG BROWN, R.E., & BARTHOLOMEW, B.,) pp. 465-478. Society for the Study of Amphibians and Reptiles, Salt Lake City.

CROTHER, B. I. (2000). Scientific and Standard English Names of Amphibians and

Reptiles of North America North of Mexico, with Comments Regarding Confidence in our Understanding. (Ed.) Society for the Study of Amphibians and Reptiles, St. Louis.

CUSHMAN, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* **128,** 231-240.

DAVIS, T.M. 1997. Non-disruptive monitoring of terrestrial salamanders with artificial cover objects on southern Vancouver Island, British Columbia. In *Amphibians in Decline: Canadian Studies of a Global Problem* (Ed. GREEN, D.M) pp.161–174. Herpetological Conservation No.1., Society for the Study of Amphibians and Reptiles, St. Louis,

DELIS, P. R., MUSHINSKY, H. R. & MCCOY, E. D. (1996). Decline of some west-central Florida anuran populations in response to habitat degradation. *Biodiversity and Conservation* **5,** 1579-1595.

EGAN, R.S., & PATON, P.W.C. (2008). Multiple scale habitat characteristics of pond-breeding amphibians across a rural-urban gradient. In: *Urban Herpetology* (eds

MITCHELL, J.C., JUNG BROWN, R.E., & BARTHOLOMEW, B.,) pp. 53-65. Society for the Study of Amphibians and Reptiles, Salt Lake City.

FULTON, W., PENDALL, R., NGUYEN, M., & HARRISON, A. (2001). Who sprawls most? How growth patterns differ across the U.S., Survey Series. The Brookings Institution Center on Urban & Metropolitan Policy. Washington, D.C.

GAGNÉ, S. A. & FAHRIG, L. (2007). Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada. *Landscape Ecology* **22,** 205-215.

GIBBS, J. P. (1998). Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* **62,** 584-589.

GIBBS, J. P., WHITELEATHER, K. K. & SCHUELER, F. W. (2005). Changes in frog and, toad populations over 30 years in New York State. *Ecological Applications* **15,** 1148-1157.

GILIOLI, G., BODINI, A., BAUMGARTNER, J., WEIDMANN, P. & HARTMANN, J. (2008). A novel approach based on information theory to rank conservation strategies: an application to amphibian metapopulations. *Animal Conservation* **11,** 453-462.

HAMER, A. J. & MCDONNELL, M. J. (2008). Amphibian ecology and conservation in the urbanising world: A review. *Biological Conservation* **141,** 2432-2449.

HECNAR, S. J. & MCLOSKEY, R. T. (1996). Regional dynamics and the status of amphibians. *Ecology* **77,** 2091-2097.

HODGKISON, S., HERO, J. M. & WARNKEN, J. (2007). The efficacy of small-scale conservation efforts, as assessed on Australian golf courses. *Biological Conservation* **135,** 576-586.

HOMAN, R. N., WINDMILLER, B. S. & REED, J. M. (2004). Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* **14,** 1547-1553.

HOULAHAN, J. E. & FINDLAY, C. S. (2003). The effects of adjacent land use on wetland amphibian species richness and community composition. *Canadian Journal of Fisheries and Aquatic Sciences* **60,** 1078-1094.

HUSTÉ, A., CLOBERT, J. & MIAUD, C. (2006). The movements and breeding site fidelity of the natterjack toad (*Bufo calamita*) in an urban park near Paris (France) with management recommendations. *Amphibia-Reptilia* **27,** 561-568.

IUCN (The World Conservation Union), 2004. 2004 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

IUCN (The World Conservation Union), 2008. 2008 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

KAREIVA, P. & WENNERGREN, U. (1995). Connecting landscape patterns to ecosystem processes. *Nature* **373,** 299-302.

KNUTSON, M. G., SAUER, J. R., OLSEN, D. A., MOSSMAN, M. J., HEMESATH, L. M. & LANNOO, M. J. (1999). Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. *Conservation Biology* **13,** 1437-1446.

LEHTINEN, R. M., GALATOWITSCH, S. M. & TESTER, J. R. (1999). Consequences of habitat loss and fragmentation for wetland amphibian assemblages. *Wetlands* **19,** 1-12.

LIPS, K. R., BREM, F., BRENES, R., REEVE, J. D., ALFORD, R. A., VOYLES, J., CAREY, C., LIVO, L., PESSIER, A. P. & COLLINS, J. P. (2006). Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences of the United States of America* **103,** 3165-3170.

LOWE, W. H. (2005). Factors affecting stage-specific distribution in the stream salamander *Gyrinophilus porphyriticus*. *Herpetologica* **61,** 135-144.

LUCK, G. W., RICKETTS, T. H., DAILY, G. C. & IMHOFF, M. (2004). Alleviating spatial conflict between people and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **101,** 182-186.

MARSH, D. M., THAKUR, K. A., BULKA, K. C. & CLARKE, L. B. (2004). Dispersal and colonization through open fields by a terrestrial, woodland salamander. *Ecology* **85,** 3396-3405.

MCCARTHY, M. A., LINDENMAYER, D. B. & DRECHSLER, M. (1997). Extinction debts and risks faced by abundant species. *Conservation Biology* **11,** 221-226.

MCKINNEY, M. L. (2002). Urbanization, biodiversity, and conservation. *Bioscience* **52,** 883-890.

MCKINNEY, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127,** 247-260.

MENSING, D. M., GALATOWITSCH, S. M. & TESTER, J. R. (1998). Anthropogenic effects on the biodiversity of riparian wetlands of a northern temperate landscape. *Journal of Environmental Management* **53,** 349-377.

MILLER, J.E., HESS, G.R., & MOORMAN, C.E. (2007). Southern two-lined salamanders in urbanizing watersheds. *Urban Ecosystems* **10,** 73-85.

MITCHELL, J.C., JUNG BROWN, R.E., & BARTHOLOMEW, B. (2008). Urban Herpetology. Society for the Study of Amphibians and Reptiles. Salt Lake City.

NOËL, S., OUELLET, M., GALOIS, P. & LAPOINTE, F. J. (2007). Impact of urban fragmentation on the genetic structure of the eastern red-backed salamander. *Conservation Genetics* **8,** 599-606.

OLSON, D. M., DINERSTEIN, E., WIKRAMANAYAKE, E. D., BURGESS, N. D., POWELL, G. V. N., UNDERWOOD, E. C., D'AMICO, J. A., ITOUA, I., STRAND, H. E., MORRISON, J.

C., LOUCKS, C. J., ALLNUTT, T. F., RICKETTS, T. H., KURA, Y., LAMOREUX, J. F., WETTENGEL, W. W., HEDAO, P. & KASSEM, K. R. (2001). Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience* **51,** 933-938.

OSTERGAARD, E.C., RICHTER, K.O., & WEST, S.D. (2008). Amphibian use of stormwater ponds in the Puget Lowlands of Washington, USA. In: *Urban Herpetology* (eds MITCHELL, J.C., JUNG BROWN, R.E., & BARTHOLOMEW, B.,) pp. 259-270. Society for the Study of Amphibians and Reptiles, Salt Lake City.

PALOSKI, R.A. (2008). Relationship between lakeshore development and frog populations in central Wisconsin. In: *Urban Herpetology* (eds MITCHELL, J.C., JUNG BROWN, R.E., & BARTHOLOMEW, B.,) pp. 77-83. Society for the Study of Amphibians and Reptiles, Salt Lake City.

PARRIS, K. M. (2006). Urban amphibian assemblages as metacommunities. *Journal of Animal Ecology* **75,** 757-764.

PATON, P.W.C., MCDONOUGH, C., & MONTIETH, K.E. (2008). Migration ecology of spotted salamanders (*Ambystoma maculatum)* on golf courses in southern New England. In: *Urban Herpetology* (eds MITCHELL, J.C., JUNG BROWN, R.E., & BARTHOLOMEW, B.,) pp. 293-301. Society for the Study of Amphibians and Reptiles, Salt Lake City.

PEARL, C. A., ADAMS, M. J., LEUTHOLD, N. & BURY, R. B. (2005). Amphibian occurrence and aquatic invaders in a changing landscape: Implications for wetland mitigation in the Willamette Valley, Oregon, USA. *Wetlands* **25,** 76-88.

PETRANKA, J. W. (1998). Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC.

PILLSBURY, F. C. & MILLER, J. R. (2008). Habitat and landscape characteristics underlying anuran community structure along an urban-rural gradient. *Ecological Applications* **18,** 1107-1118.

POUNDS, J. A., BUSTAMANTE, M. R., COLOMA, L. A., CONSUEGRA, J. A., FOGDEN, M. P. L., FOSTER, P. N., LA MARCA, E., MASTERS, K. L., MERINO-VITERI, A., PUSCHENDORF, R., RON, S. R., SANCHEZ-AZOFEIFA, G. A., STILL, C. J. & YOUNG, B. E. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439,** 161-167.

PRICE, S. J., DORCAS, M. E., GALLANT, A. L., KLAVER, R. W. & WILLSON, J. D. (2006). Three decades of urbanization: Estimating the impact of land-cover change on stream salamander populations. *Biological Conservation* **133,** 436-441.

REINELT, L., HORNER, R., & AZOUS, A. (1998). Impacts of urbanization on palustrine (depressional freshwater) wetlands—research and management in the Puget Sound region. *Urban Ecosystems* **2,** 219-236.

RICKETTS, T.H., DINERSTEIN, E., OLSON, D.M., LOUCKS, C.J., EICHBAUM, W., KAVANAGH, K., HEDAO, P., HURLEY, P., CARNEY, K.M., ABELL, R., & WALTERS, S. (1999). Terrestrial Ecoregions of North America: A Conservation Assessment. Island Press, Washington, DC.

RILEY, S. P. D., BUSTEED, G. T., KATS, L. B., VANDERGON, T. L., LEE, L. F. S., DAGIT, R. G., KERBY, J. L., FISHER, R. N. & SAUVAJOT, R. M. (2005). Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. *Conservation Biology* **19,** 1894-1907.

ROBBINS, C. S., SAUER, J. R., GREENBERG, R. S. & DROEGE, S. (1989). Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences of the United States of America* **86,** 7658-7662.

ROTHERMEL, B. B. (2004). Migratory success of juveniles: A potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications* **14,** 1535-1546.

ROTHERMEL, B. B. & SEMLITSCH, R. D. (2002). An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology* **16,** 1324-1332.

RUBBO, M. J. & KIESECKER, J. M. (2005). Amphibian breeding distribution in an urbanized landscape. *Conservation Biology* **19,** 504-511.

SCHMIDT, B. R. (2008). Steps towards better amphibian conservation. *Animal Conservation* **11,** 469-471.

SEMLITSCH, R. D. (1998). Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* **12,** 1113-1119.

SEMLITSCH, R. D. (2008). Differentiating migration and dispersal processes for pond-breeding amphibians. *Journal of Wildlife Management* **72,** 260-267.

SEMLITSCH, R. D. & BODIE, J. R. (2003). Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* **17,** 1219-1228.

SKIDDS, D. E., GOLET, F. C., PATON, P. W. C. & MITCHELL, J. C. (2007). Habitat correlates of reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed. *Journal of Herpetology* **41,** 439-450.

SMITH, M. A. & GREEN, D. M. (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* **28,** 110-128.

SODHI, N., BICKFORD, D., DIESMOS, A., LEE, T., KOH, L., BROOK, B. W., SEKERCIOGLU, C. & BRADSHAW, C. J. A. (2008). Measuring the meltdown: Drivers of global amphibian extinction and decline. *PLoS ONE* **3,** e1636. doi:10.1371/journal.pone.0001636.

STUART, S. N., CHANSON, J. S., COX, N. A., YOUNG, B. E., RODRIGUES, A. S. L., FISCHMAN, D. L. & WALLER, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science* **306,** 1783-1786.

TRENHAM, P.C. & COOK, D.G. (2008). Distributions of migrating adults related to the location of remnant grassland around an urban California tiger salamander (*Ambystoma californiense*) breeding pond. In: *Urban Herpetology* (eds MITCHELL, J.C., JUNG BROWN, R.E., & BARTHOLOMEW, B.,) pp. 33-40. Society for the Study of Amphibians and Reptiles, Salt Lake City.

WARKENTIN, I. G., BICKFORD, D., SODHI, N. & BRADSHAW, C. J. A. (2009). Eating frogs to extinction. *Conservation Biology*.

WESTMACOTT, R. (1991). Scale economics – ecological theory and planning practice in urban landscapes. *Landscape and Urban Planning* **21,** 21-29.

WIENS, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**: 385-397.

WILLSON, J. D. & DORCAS, M. E. (2003). Effects of habitat disturbance on stream salamanders: Implications for buffer zones and watershed management. *Conservation Biology* **17,** 763-771.

WINDMILLER, B.S., & CALHOUN, A.J.K. (2008). Conserving vernal pool wildlife in urbanizing landscapes. In: Science and conservation of vernal pools in Northeastern North America. (Eds CALHOUN, A. J. K., & DEMAYNADIER. P.G) pp. 233-251. CRC Press, Boca Rotan.

WINDMILLER, B.S., HOMAN, R.N., REGOSIN, J.V., WILLETTS, L.A., Wells, D.L., & Reed, J.M. (2008). Breeding amphibian population declines following loss of upland forest habitat around vernal pools in Massachusetts, USA. In: Mitchell, J.C., Jung Brown, R.E., Bartholomew, B., (Eds.), Urban Herpetology. Society for the Study of Amphibians and Reptiles, Salt Lake City, pp. 41-51.

WOODFORD, J. E. & MEYER, M. W. (2003). Impact of lakeshore development on green frog abundance. *Biological Conservation* **110,** 277-284.

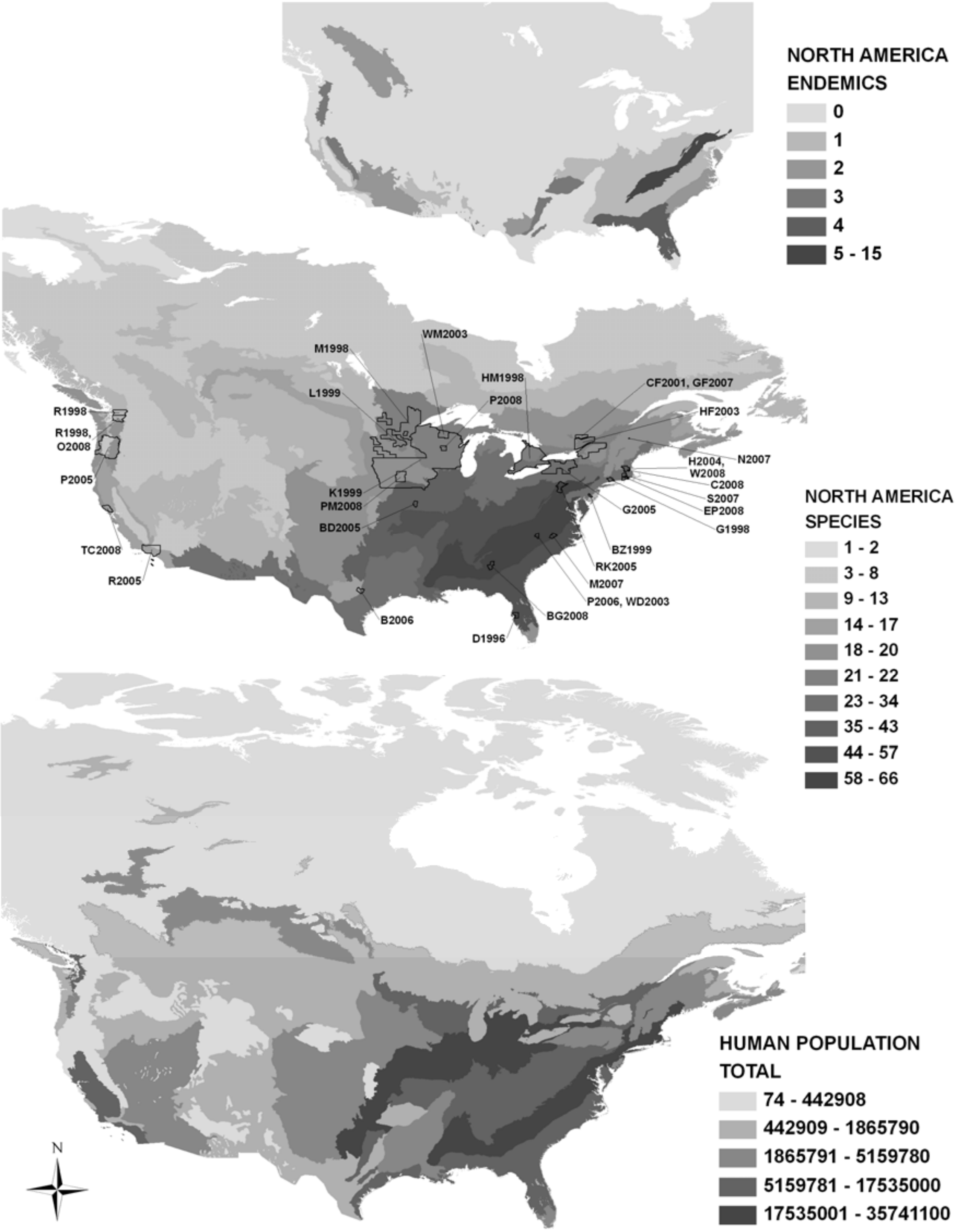

Fig. 2.1 Maps of amphibian species endemism (*Upper*), richness (*Middle*) and year 2000 human population counts (*Lower*) by terrestrial ecoregions for North America (Olson et al. 2001). The outlined areas on the North American species map (*Middle*) represent the sites of 32 urban studies. Each site is labeled with the first letter of author(s) name and year.

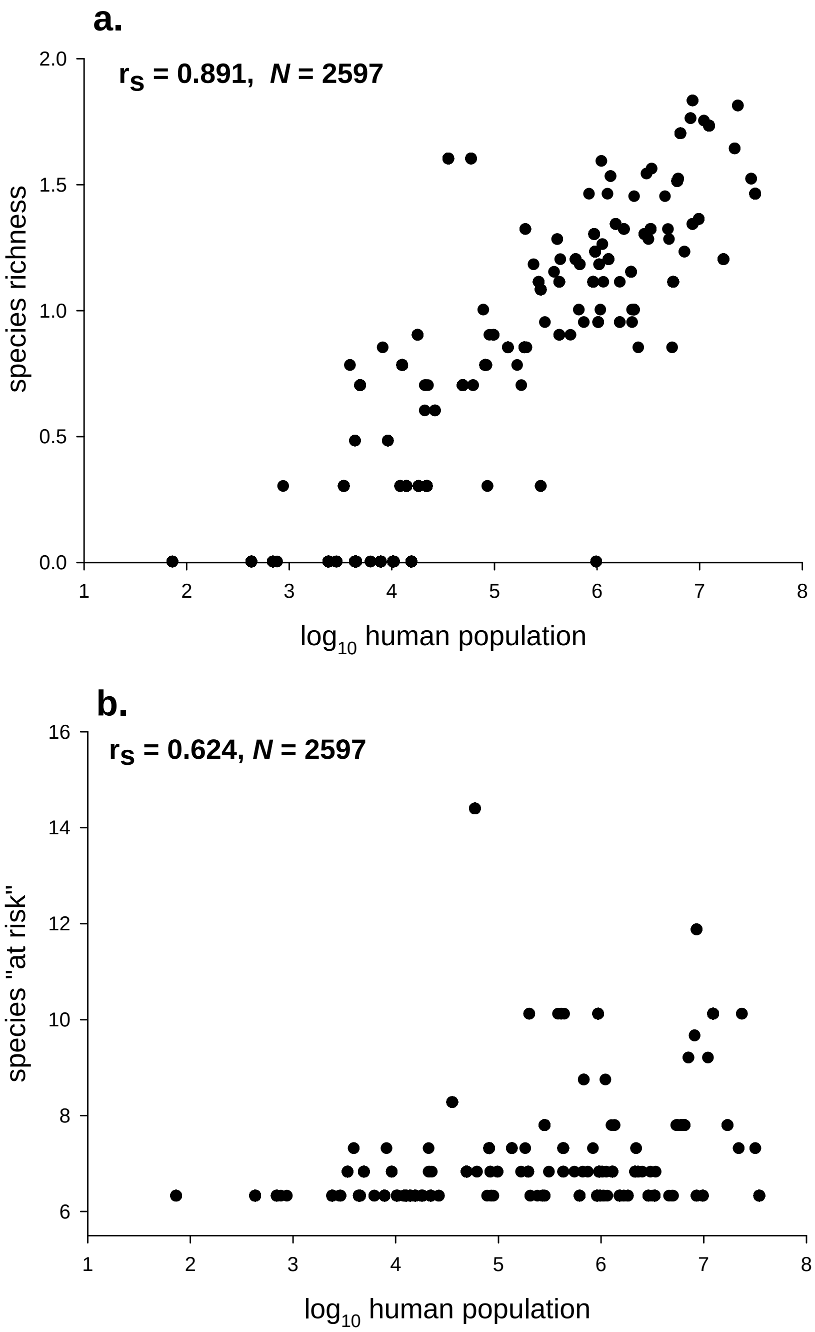

Fig. 2.2a and b Correlation between [logarithm$_{10}$] human population counts and [power transformed $(X + 10)^P$)] amphibian species richness (a: *Upper*) and [logarithm$_{10}$] human population counts and [power transformed $(X + 10)^P$] number of species "at risk" (b: *Lower*) for all terrestrial ecoregions in North America.

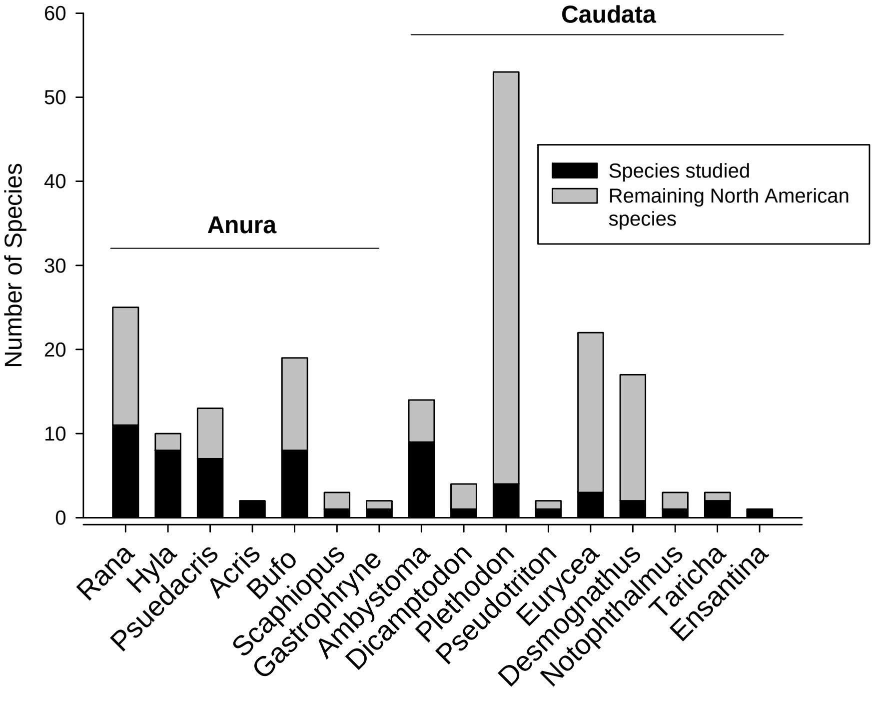

Fig. 2.3 The number of species (*N* = 62) for each genus investigated in urban environments by 32 studies conducted between 1990 and 2008 compared to the number of North American species not studied for each genus (*N* = 261).

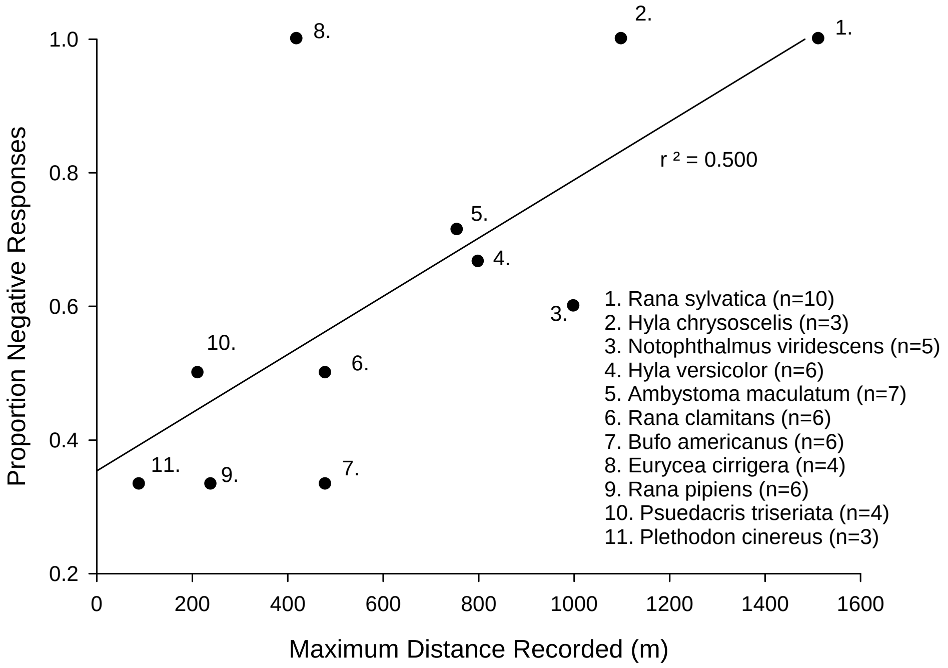

Fig. 2.4 The response to urbanization by 11 North American amphibian species in relation to their maximum recorded movement distance. As the maximum movement distance increases, more studies ($N = 3$ to 10) report a "negative" association with urbanization. Each point represents a species (labeled #1-11).

Table 2.1. The number of species considered in 32 urban studies in North America. The heading A/C represents whether study considered Anura (A), Caudata (C) or both (A & C).

Paper	Location	A/C	Species #
Barrett and Guyer 2008	Georgia, USA	A & C	17
Birchfield and Deters 2005	Missouri, USA	A	1
Bowles et al. 2006	Texas, USA	C	1
Bunnell and Zampella 1999	New Jersey, USA	A	10
Carr and Fahrig 2001	Ontario, Canada	A	2
Clark et al 2008	Massachusetts, USA	A & C	2
Delis et al. 1996	Florida, USA	A	16
Egan and Paton 2008	Rhode Island, USA	A & C	2
Gagńe and Fahrig 2007	Ontario, Canada	A	10
Gibbs 1998	Connecticut, USA	A & C	5
Gibbs et al. 2005	New York State, USA	A	5
Hecnar and M'Closkey 1998	Ontario, Canada	A & C	13
Homan et al. 2004	Massachusetts, USA	A & C	2
Houlahan and Findlay 2003	Ontario, Canada	A & C	13
Knutson et al. 1999	Iowa and Wisconsin, USA	A	14
Lehtinen et al. 1999	Minnesota, USA	A & C	10
Mensing et al. 1998	Minnesota, USA	A	5
Miller et al. 2007	North Carolina, USA	C	1
Noël et al. 2007	Québec, Canada	C	1
Ostergaard et al. 2008	Washington, USA	A & C	6
Paloski 2008	Wisconsin, USA	A	8
Pearl et al. 2005	Oregon, USA	A & C	6
Pillsbury and Miller 2008	Iowa, USA	A	7
Price et al. 2006	North Carolina, USA	C	2
Reinelt et al. 1998	Washington, USA	A & C	10
Riley et al. 2005	California, USA	A & C	5
Rubbo and Kiesecker 2005	Pennsylvania, USA	A & C	11
Skidds et al. 2007	Rhode Island, USA	C	2
Trenham and Cook 2008	California, USA	C	1
Willson and Dorcas 2003	North Carolina, USA	C	2
Windmiller et al. 2008	Massachusetts, USA	A & C	3
Woodford and Meyer 2003	Wisconsin, USA	A	1

Table 2.2. The total number of species-specific responses (negative, positive, neutral, and unknown) collated by genus for 32 urban studies.

		Total Responses			
Genus	Number of Species	negative	positive	neutral	unknown
Rana	11	18	2	12	35
Hyla	8	12	0	2	8
Psuedacris	6	7	1	6	12
Acris	2	2	0	0	3
Bufo	8	4	3	4	10
Scaphiopus	1	1	0	0	0
Gastrophryne	1	0	0	1	0
Eleutherodactylus	1	1	0	0	0
All Anura	38	45	6	25	68
Ambystoma	9	7	0	6	9
Dicamptodon	1	0	0	0	1
Plethodon	4	3	0	2	1
Pseudotriton	1	1	0	0	0
Eurycea	3	6	0	0	0
Desmognathus	2	3	0	0	0
Notophthalmus	1	3	0	2	
Taricha	2	1	0	0	3
Ensantina	1	0	0	0	1
All Caudata	24	24	0	10	15
All Amphibian Species	62	69	6	35	83

Table 2.3. The breeding habitat for frog and salamander species studied in urban literature compared to the breeding habitats for all North American salamanders and frogs.

	Breeding Habitat							
	Wetland/Temporary Pools	Stream/Springs	Terrestrial	Wetland/Stream	Wetland/Terrestrial	Cave	Unknown	Total
All North American salamanders	19	45	78	10	2	11	1	166
Urban literature salamanders	9	6	5	4	0	0	0	24
% sal. studied (urban / total)	47	13	6	40	0	0	0	14
All North American frogs	66	7	7	12	0	0	3	95
Urban literature frogs	32	0	1	5	0	0	0	38
% frogs studied (urban / total)	48	0	14	42	0	0	0	40
North American total amphibians	85	52	85	22	2	11	4	261
Urban literature total amphibians	41	6	6	9	0	0	0	62
% amphib. studied (urban / total)	48	12	7	41	0	0	0	24

Chapter 3

The value of stormwater wetlands as habitat for multiple life-history stages of the wood frog (*Lithobates sylvaticus*) in an urbanized landscape

INTRODUCTION

Urbanization is a pervasive disturbance that threatens amphibian populations worldwide. Numerous studies document the correlation between urbanization and decreases in amphibian species richness and abundance, and overall decreases in population persistence at the landscape scale (Hamer and McDonnell 2008), all of which are especially pronounced for species requiring upland habitats after breeding (Pillsbury and Miller 2008). While negative impacts of urbanization on amphibian populations are generally recognized, little is known about which life-history stages, aquatic or terrestrial, are most affected by urbanization.

Pond-breeding amphibians require both aquatic habitat to reproduce and terrestrial habitat to feed, and overwinter (Semlitsch and Bodie 2003). Having dual habitat requirements makes amphibians doubly susceptible to disturbances because alterations to either habitat could negatively affect a population. In urban environments, identifying the habitat that limits population size is unclear because terrestrial habitats are often considerably altered by human development and natural aquatic habitats are often destroyed and replaced by stormwater wetlands. Throughout the world (e.g., USA, Denmark, Taiwan), constructed stormwater wetlands have become increasingly common over the past 30 years (Bhamidimarri et al. 1991, Brix 1994, Smith 2009). In highly urbanized landscapes, stormwater wetlands function as collection sites for highway particulate (e.g., highway salt) and other pollutants, which could lower the reproductive success of amphibians that use these wetlands to breed (Snodgrass et al. 2008, Camponelli et al. 2009). Similarly, native terrestrial habitats (e.g., forest) are often removed and replaced with impervious surfaces and manicured lawns, a process that negatively affects adult amphibians (McKinney 2002, Gibbs et al. 2005, Riley et al. 2005). Little is known, however, regarding the suitability of stormwater wetlands or urban terrestrial environments as habitat for various life stages.

Although research suggests that stormwater wetlands do provide aquatic habitat for breeding for some species (Simon et al. 2009), these studies typically only examine adult life history stages (e.g., record calling males or use egg masses to quantify presence and abundance of females) or combine multiple life stages (e.g., calling males, eggs and larvae) into a single metric of occurrence (e.g., Ostergaard et al. 2008 and Lehtinen et al. 1999). Because few studies specifically examine larvae and newly metamorphosed terrestrial life stages, it is not known whether populations at stormwater wetlands are capable of reproductive recruitment (as defined by the presence of terrestrial young-of-the-year and not just larvae which may die prior to metamorphosis) versus populations that unsuccessfully recruit individuals but are instead sustained through immigration (e.g., stormwater wetlands functioning merely as “sinks” or “ecological traps”; Battin 2004). Additionally, if recruitment does occur at stormwater wetlands, how do these individuals compare with metamorphs produced by natural systems?

Amphibians have the potential to be regulated (i.e., control population size) at multiple life-history stages (Goater 1994, Harper and Semlitsch 2007, Loman and Lardner 2009). Understanding the interplay between habitat and life-history, and how this interaction affects populations is essential for devising sound conservation strategies. For amphibians, larval traits, particularly size at metamorphosis, are closely associated with survival and reproductive success of subsequent life stages (Semlitsch et al. 1988). Specific biotic and abiotic features of aquatic systems may affect growth rates and larval performance. For example, predation risk and low food both depress larval growth (Werner and Anholt 1996, Newman 1998). In addition, individuals reared under high larval densities exhibit decreased clutch-size, smaller size at first reproduction, and greater age at first reproduction as adults (Smith 1987, Goater 1994, Scott 1994).

Wetland type may also affect the size of larvae. For example, Skelly et al. (2002) found that wood frog larvae in Connecticut, USA, grew slower in closed-canopy wetlands versus open-canopy wetlands, and attributed slower growth to lower water temperature. Considering the influence of wetland type on the physical traits of larvae, constructed stormwater wetlands in urban environments may possess particular abiotic and biotic factors, such as high heavy metal concentrations or exotic species (Adams 2000, Sharma and Patiño 2009), that adversely affect larval performance. These factors could decrease recruitment and size of the local population, even though adequate terrestrial habitat is maintained surrounding these wetlands.

Conversely, certain attributes of stormwater wetlands may be favorable to larval growth (e.g., decreased larval density), by providing survival and reproductive advantages to individuals in urban amphibian populations. These wetland-based advantages may be negated if sufficient terrestrial habitat is not maintained during the course of urban development to support required overwintering and foraging habitat for pond-breeding amphibians. Additionally, limited terrestrial habitat, causing individuals to congregate in small habitat patches could cause density dependent regulation at the terrestrial life phase (Harper and Semlitsch 2007, Patrick et al. 2008).

In the present study, I characterize the amphibian assemblage that uses stormwater wetlands in Edmonton, Alberta, Canada and focus on the population biology of the wood frog (*Lithobates sylvaticus*) by assessing whether stormwater wetlands provide habitat for multiple life-history stages of this species.

Of the assemblage of pond breeding amphibians in North America (i.e., those species that have both aquatic and terrestrial habitat requirements), the wood frog has one of the largest geographic ranges. Wood frog is a forest-dependent species and typically spends only a few weeks at wetlands to breed (Rittenhouse and Semlitsch 2007b). The remainder of the annual cycle is spent in surrounding terrestrial habitat (Rittenhouse and Semlitsch 2007b). Wood frogs migrate and disperse to and from breeding wetlands into surrounding terrestrial habitat, thus intact terrestrial habitat surrounding breeding wetlands is imperative for long-term population persistence (Semlitsch 1998, Smith and Green 2005). Wood frog is an appropriate focal species for studying whether forest dependent amphibians will use permanent urban stormwater wetlands as habitat. Lastly, numerous studies have investigated the general biology of the wood frog at both aquatic and terrestrial life-stages and provide a good framework for examining multiple life-history stages in urban landscapes (see Amphibia Web 2009 for a list of studies on wood frog).

Five species of amphibian (wood frog (*Lithobates sylvaticus*), boreal chorus frog (*Pseudacris maculata*), boreal toad (*Anaxyrus boreas*), Canadian toad (*Anaxyrus hemiophrys*), and gray tiger salamander (*Ambystoma malatovorium*) occur within my study region (Russell and Bauer 2000). I first determined which of these species occurred at stormwater wetlands. I also surveyed natural wetlands located within urban environments for comparison with constructed sites. I predicted each of the five species would occur at a higher proportion of natural wetlands in upland areas and in the North Saskatchewan River valley than constructed stormwater wetlands. Additionally, I predicted all species would be present in higher abundances at natural wetland types. Abiotic conditions in the aquatic environment could affect breeding site selection by adults and influence larvae and metamorph performance; I therefore examined temperature, chlorophyll-a, and other within-pond variables (e.g., trace elements, submersed aquatic vegetation, etc.) for stormwater and natural wetlands.

Based on the terrestrial habitat requirements of the wood frog I expected adult occurrence to be best predicted by the proportion of local native vegetation (e.g., vegetation within 10 – 30 m of wetlands versus native vegetation at landscape scales (1000 m)) surrounding breeding habitat. Although I predict that stormwater wetlands will provide habitat for all life-history stages, I hypothesize that wood frogs will occur on a larger proportion of natural wetlands and at higher relative abundances for all life stages. These hypotheses are based on preliminary observations made prior to the beginning this study, as well as literature which suggests that urbanization adversely affects amphibians (Hamer and McDonnell 2008). Additionally, I propose that metamorphs will be larger in natural wetlands because of more favorable environmental conditions such as lower heavy metal concentrations and warmer water typical of shallow wetlands. The "optimal" environmental conditions characteristic of natural wetlands should enhance larval growth and result in increased body size at metamorphosis (Alford and Harris 1988). Lastly, based on the results of my study, I discuss whether stormwater wetlands can be used to maintain local amphibian populations and whether the study of multiple life-history stages provides useful information for managing urban amphibian populations.

METHODS

Study Area

My study occurred within the City of Edmonton, located in north-central Alberta, Canada (Fig. 3.1; 53°32'27" N, 113°29'37" W). Edmonton, one of the fastest growing cities in Canada (approximately 1.1 million people in 2008), is home to the largest protected urban park system (7400 ha) in North America (City of Edmonton; www.edmonton.ca). The North Saskatchewan

River valley bisects the city and is a major component of this park system. The City of Edmonton exists at an ecotone between the Aspen Parkland and the Boreal Mixed-wood Forest (Royer and Dickinson 2007). The dominant native trees are *Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera* interspersed with patches of *Picea mariana* and *Picea glauca*. Presently, 71.5% of existing natural areas within both the river valley and tablelands are unprotected, and 21% of the remaining native habitats in the tableland have been lost to development since 1993 (Natural Connections Strategic Plan 2007). It is estimated that 85 to 95% of the original Aspen Parkland has been lost to agriculture and urbanization (Alberta Environmental Protection 1997).

One man-made and two naturally occurring wetland types exist within Edmonton: constructed stormwater wetlands, natural upland wetlands, and natural river valley oxbow wetlands. Stormwater wetlands were primarily constructed for flood prevention and to sequester pollutants from surface runoff. They have an average size of 16402 m^2 ± 12568 SD (Table 3.1). Most were created since the mid 1990s (Drainage Services, City of Edmonton; Table 3.1). Upland wetlands are the predominant naturally occurring wetland type in the city with an average size of 16349 m^2 ± 28006 SD (Table 3.1). The upland wetlands are characterized as Class III-V seasonal to permanent wetlands as they can fluctuate in hydroperiod with extended drought or above-normal precipitation (Stewart and Kantrud 1971). These open water marshes have no inlets or outlets and are fed by either ground or surface water. River valley wetlands are typically U-shaped oxbow lakes and have an average size of 3424 m^2 ±2668 SD. They are formed by meandering streams and are primarily located in ravines throughout the city. Hydroperiod ranges from permanent for stormwater wetlands, and semi-permanent to seasonal for river valley and upland wetlands. Seasonal hydroperiods are characterized by a continuum that varies with wetland size and depth, but I observed that most seasonal to semi-permanent wetlands drew down to their lowest level (completely dry or puddles) by late summer and typically recharged with spring snowmelt. Additionally, most wetlands in this study area are likely devoid of fish from frequent winterkill events (Danylchuk and Tonn 2003), even though some wetlands may experience fish colonization (e.g., river valley oxbow wetlands reconnect with streams during flood events).

Breeding-Call Surveys

During the spring of 2008 and 2009, I surveyed 75 bodies of water (58 stormwater, 12 natural upland, and 5 river valley wetlands) throughout Edmonton. I documented the occurrence of amphibian species in order to identify the composition of assemblages throughout Edmonton's urban wetlands.

Breeding Call Surveys (BCS) for anurans began at ice-off and followed methodologies outlined in Stevens and Paszkowski (2004). In 2008, BCSs occurred from April 29 to May 15 and each wetland was surveyed once. In 2009, BCSs occurred from April 30 to May 18 and all wetlands were surveyed two to three times. Surveyed wetlands varied in size from 0.05 to 10.3 ha. Prior to each survey, one or two researchers walked the wetland perimeter (15 m from shore to avoid disturbance) and stopped every 100 m to listen for calling males (Woodford and Meyer 2003). The initial survey point was established in areas that contained calling frogs. From this starting point, I conducted the remaining point counts at 100 m intervals (maximum four points per wetland). If no males were heard calling, I conducted point counts every 100 m, starting at a random point, for a maximum of four points per wetland. Smaller wetlands required fewer points, with a minimum of one point. I conducted surveys within a 3 hour period (between approximately 2100 and 2300 hrs). Surveys started 0.5 hours after sunset under optimal weather conditions (i.e., light or no rain, Beaufort Wind Scale < 4, air temperature > 5°C; Shirose et al. 1997).

At each point I conducted a 180º point count for 5 minutes to record all frogs heard within 50 m. Each observer estimated the total number of calling males at each point and assigned a rank: Rank 0 = no calling frogs, Rank 1 = no distinct overlap in calls and males abundances can be reliably estimated, Rank 2 = some overlap in calls and the number of males can be estimated (but less accurately than for Rank 1), and Rank 3 = significant overlap in calls and the individuals cannot be estimated (Weir 2001, Stevens and Paszkowski 2004).

Six wetland sites were chosen for multiple BCS sampling during the survey period in 2008 to account for temporal variation in numbers of calling males and to identify the peak calling-period. To account for potential temporal variation in calling, surveys of wetlands in 2009 were conducted in the opposite order from surveys in 2008. Additionally, BCSs (2008 and 2009) were conducted at representatives of each wetland type throughout the survey period to correct for false differences that may occur if all representatives of one wetland type were sampled first (pre-peak) or last (post-peak). Because there were fewer river valley and upland wetlands than survey nights, we were unable to survey all wetland types on each night; therefore, wetlands were visited evenly throughout the entire survey period. Because precipitation influences both the hydrology (i.e., quality) of breeding habitat as well as amphibian behavior, I acquired daily precipitation data (collected by Edmonton's Office of Asset Management and Public Works) from late April to late October (2008 and 2009) for three wetland locations (located in the east, west and south of our study area). Rain was recorded by Texas Electronics TR-525M tipping bucket style rain gauges.

Measurement of Wetland Environmental Features

I quantified multiple within-wetland variables for 73 of 75 study wetlands from late July to mid August, 2008. For each wetland I recorded maximum water depth. All stormwater wetlands were constructed with a standard maximum water depth of 220 cm (Drainage Services, City of Edmonton). Because aquatic vegetation structure can influence multiple amphibian life-history stages (e.g., egg mass deposition, selection of egg-laying sites within wetlands as well as size of larvae at metamorphosis), I quantified emergent vegetation and submersed aquatic vegetation (SAV) for each wetland (Egan and Paton 2004, Skidds et al. 2007, Purrenhage and Boone 2009). At wetlands that had calling wood frogs in April and May, I conducted emergent plant surveys from late July to mid August, in areas where calling had occurred, in order to describe habitat previously occupied by breeding frogs. For wetlands with no calling frogs, sampling occurred at BCS points. All wetlands had a total of four survey points. If wetlands had less than four BCS points, I surveyed at each BCS point and all remaining points (up to four) were taken at cardinal directions to reduce bias. A rank (1-5) was assigned for emergent vegetation: (1) no plant cover observed (0%), (2) rare plant cover (<5%), (3) occasional plant cover (5%-25%), (4) common plant cover (25%-75%), and (5) abundant plant cover (>75%) (Bayley and Prather 2003).

From late July to mid August, submersed aquatic vegetation (SAV) was measured at four points for each wetland (determined by cardinal directions). I quantified SAV growth for a 1 m^2 area for each point. The sampling area for each point was chosen in a random direction 1 m from the center of each SAV zone. If the SAV zone was not visible, I randomly selected a point 2 m from the end of the emergent zone. If neither an emergent nor SAV zone was detectable, I chose a point 5 m from shore. For each 1 m^2 sample plot, I measured the total water depth, depth of SAV, and depth of open water column for five points, four at each corner and one at the center.

Using a 1 m^2 grid, I visually estimated the percent area covered by SAV. The 1 m^2 sampler was made of a square floating quadrat divided into 100 10 cm^2 sections. Submersed aquatic vegetation excluded emergent floating-leaved macrophyte species (Bayley and Prather 2003).

To measure potential differences in within-pond habitat between wetland types, I measured several water chemistry parameters that might affect breeding site selection by adult frogs or larvae development. Stormwater wetlands may contain higher levels of heavy metals in sediments (e.g., arsenic, cadmium, chromium, zinc and lead) than naturally present. Both low (<5.5) and high (>8.5) pH has been shown to lower survivorship, growth and development rates of wood frog larvae and other amphibian species, as well as cause malformations and compromised swimming performance (Abbasi et al. 1989, Horne and Dunson 1995, Raimondo et al. 1998, Hopkins et al. 2000, Snodgrass et al. 2008). I also recorded nitrogen and phosphorus concentrations in all wetland types as an indicator of potential fertilizer run-off. High levels of nitrogen (e.g., nitrogen pollution from fertilizer run-off) may adversely affect both larvae and adult amphibians (Rouse et al. 1999, Camargo et al. 2005, Earl and Whiteman 2009) and wood frog occurrence was negatively related to plant nutrients (both nitrogen and phosphorus) in 74 wetlands in Ontario, Canada (Houlahan and Findlay 2003). However, nitrogen and phosphorus concentrations may not strongly influence frogs in Edmonton, as most naturally occurring wetlands in the area are naturally eutrophic or even hypereutrophic. For example, Anderson et al. (2002) found that over 75% of semi-permanent wetlands in the Aspen Parkland of Alberta were hypereutrophic based on phosphorus concentrations (>100 μg/L).

Water chemistry samples (Tables 3.1 and 3.2) were collected from July 20 through August 20, 2008. Water was collected from the center of open-water areas (typical depth ≥ 120 cm) from one of the four BCS point counts, which were chosen at random. Samples were stored on ice and transported to the Biogeochemical Analytical Laboratory, University of Alberta for analysis. All volatile compounds were analyzed within 24 hours of collection.

Landscape Classification and Spatial Analyses

I compared the presence/absence of calling male frogs to proportion of native vegetation cover at multiple spatial scales in order to identify the scale that best predicts wood frog occurrence at urban wetlands in the study area. Geospatial analyses were completed using the ArcGIS 9.2x software package (Environmental Systems Research Institute, Redlands, CA). I mapped nine land-use types within the study area and then grouped them into five cover types: 1) impervious (e.g., roads, parking lots, commercial buildings), 2) nonforest manicured (e.g., mowed grass, sports and recreation fields), 3) barren ground (area of land with topsoil removed in preparation for development), and 4) residential (includes all houses as well as the land between houses (i.e., grass lawn, shrubs, etc)) were grouped as “urban”; 5) agriculture; 6) river (1^{rst}-3^{rd} order streams); 7) wetlands (all three types: upland, river valley, and stormwater) and 8) mixed-wood forest and shrubland (areas of tall grass mixed with shrubs) were grouped as native vegetation. All land-use types were mapped using aerial photo interpretation (1:20,000 scale) from 0.25-m resolution black and white digital orthophotos (leaf-off) taken in April/May 2007 and produced by Land Data Technologies Inc. under the City of Edmonton Regional Joint Ortho Initiative. I mapped wetland area with imagery from immediately after snow melt, thus all wetlands were most likely at maximum depth and area.

If land cover was ambiguous, I used high-resolution color imagery from Google Earth images to aid in classification (Google Earth v4.3; http://earth.google.com). I created an error matrix to assess the accuracy of my mapping. I generated one randomly placed point *post hoc* per 1 km² for all land-use types. A second round of classification was conducted at each point to determine the accuracy for original mapping classifications. I had an overall accuracy of 94%. All cover types were mapped within 1000 m of each wetland. I chose this distance because it is representative of dispersal and migration distances for pond-breeding amphibians (Berven and Grudzien 1990, Semlitsch 1998).

According to Wiens (1989), scale has two components, extent and grain. Extent is the spatial area defined as the landscape, and grain (or resolution) is the smallest area for which the study has values or characteristics. In order to identify the zone that best predicted wood frog occurrence, I generated concentric zones based on 10 m, 50 m, and 100 m intervals (i.e., grain size) between 0-1000 m (i.e., extent) surrounding each wetland (similar to Pellet et al. 2004) (Fig. 3.2). I chose the 10 m interval because many, but not all, stormwater wetlands in the study have small scale riparian buffers (mostly consisting of tall grass) that typically are between 5-25 m in width (Scheffers, unpublished data). Larger intervals of 50 and 100 m were chosen to represent intermediate and landscape scales, respectively (Pellet et al. 2004, Pearl et al. 2005).

Egg Mass Surveys

In 2008, during daylight hours, in coordination with breeding call surveys (April-May), I conducted egg-mass counts at the 43 wetlands where wood frogs were heard calling during BCS (Skidds et al. 2007). Each wetland was surveyed once. Each individual female wood frog deposits one gelatinous egg mass either at a communal deposition site or singly (Crouch and Paton 2000). An assumption of a 1:1 egg mass-to-female ratio provides relatively accurate estimates of females' annual breeding effort (Skidds et al. 2007). Egg mass counts were performed by visually searching wetland margins and in shallow water ≤ 1 m deep. For large clusters of egg masses, counts were performed three times and averaged. All masses were flagged to avoid double counting and for future sampling of aquatic larvae. A relative abundance of egg masses was generated for each wetland and consisted of the total number egg masses.

In 2009, I conducted egg mass surveys at a subset of 15 focal wetlands as part of my effort to compare metamorph size among wetland types. In order to quantify breeding effort by females, I conducted egg mass surveys (April – May) at each wetland four times from first date of egg deposition. Each mass or cluster was flagged to prevent double counting. Surveys were conducted at seven stormwater, five river valley, and three upland wetlands, however, one river valley and one stormwater wetland were excluded immediately after initial counts because of drying (river valley) and human disturbance (stormwater). These 13 focal wetlands were selected from a stratified random sample of all BCS wetlands that contained calling male frogs and egg masses in 2008. This approach increased the likelihood that tadpoles and metamorphs would be present during later surveys. I chose multiple wetlands of each type to ensure replication, but was constrained to 13 sites due to the time required for repeated sampling. All focal wetlands had open canopies, thus allowing relatively equal amounts of solar exposure.

Tadpole Surveys

In June and July 2008, I set minnow traps (44.5 cm. long, 22.9 cm high, with 0.63 cm^2 galvanized wire mesh) for larvae at 39 wetlands that had calling male wood frog during BCS. As noted, egg-mass locations were flagged during previous surveys. I tried to sample at least one wetland of each type on each of 22 sampling dates. Six minnow traps were used to survey egg-mass locations. If a wetland contained both individual and egg-mass clusters, traps were placed in the area surrounding clusters. For a wetland with multiple egg mass locations, a maximum of two clusters and two single egg masses were sampled per wetland (total of four sampling arrays). A two trap array was used to sample locations without egg masses in order to account for nondetection of egg masses from previous egg mass surveys. Traps were checked every two days. In order to prevent tadpole asphyxiation, all traps were attached to a stake so that some portion of the trap was suspended above water. I generated an average relative abundance of tadpoles for each of the 39 wetlands surveyed. Relative abundance for each wetland was based on the total number of individuals caught per total traps for each wetland. Wetlands were sampled between 1 and 10 times. Upland, river valley and stormwater wetland sites that were more extensively sampled were done so to account for potential temporal variation in tadpole numbers. Because of few visits and low catches at some wetland sites, I pooled data for all traps rather than recording values on a per survey basis.

From early mid-June to July 2008, in conjunction with my tadpole surveys of BCS wetlands, three wetlands (two stormwater wetlands and one natural upland site) were sampled every two days to assess preliminarily tadpole abundance between wetland types. I continuously sampled these wetlands to determine tadpole relative abundances under high sampling effort. Overall relative abundance was recorded as number of tadpoles per minnow trap.

Between May and July 2009, I conducted tadpole surveys once a week at the subset of 13 wetlands previously surveyed for egg masses using dipnets (17.5 in. x 16 in.) to capture tadpoles. I constrained sampling to 30 minutes and recorded total dipnet attempts. Tadpoles were captured by walking the wetlands edge and sampling from bank-line to depths < 1 m. I calculated tadpole relative abundance for every survey based on the number of individuals caught per dipnet sweep (average of 110 dips per survey ± 59 SD).

Metamorph Surveys

In 2008, I incidentally noted the presence of metamorphs at all 75 BCS wetlands surveyed for wetland environmental features (see above). Each wetland was surveyed once from mid-July through late August. Additionally, I used drift fences (approximately 3 m in length and 1m in height, made of silt fencing) at two stormwater (Wetland S106 = eight fences and Wetland S108 = 12 fences), one river valley (Wetland RV315 = eight fences) and one upland wetland (Wetland U410 = five fences) to capture emigrating metamorphs between early July and the end of September. Four buried plastic buckets (35 cm deep, 15 cm in diameter) accompanied each fence. Drift fences were placed at the edge of the riparian zone (between 5 and 25 m from the water's edge), spaced 50 m apart, and checked every two days.

In 2009, from mid-July through August, two to four rounds of visual surveys for metamorphs were conducted at all 45 BCS wetlands where calling male frogs were heard in spring. During the same period of time, I also sampled for metamorphs once a week at my subset of 13 wetlands in order to monitor metamorph size for the three wetland types. Searches were conducted within 5 m of the shoreline. Exact duration was recorded for each visual search, but constrained to 30 to 60 min depending on wetland size. Each focal wetland was sampled a total of three times. Prior to metamorph surveys, I monitored larvae development at the 13 focal wetlands in order to identify approximate times of metamorphosis. As part of my 2009 tadpole surveys I began sampling for tadpoles several weeks prior to metamorph surveys and was therefore able to identify the development stage of tadpoles throughout my study area. I began my surveys when the first tadpole at Gosner stage 42-43 was found (Gosner et al 1960). This ensured that I sampled newly metamorphosed individuals. Individuals are considered metamorphs when at Gosner stage 46, and characterized by size (making metamorphs apparently different than juveniles), and contained adult non-larval characteristics. I calculated a single relative abundance of metamorphs as the total number of individuals caught per total number of minutes of search for all surveys. In order to identify potential variability in relative abundance across the season, for each wetland type, I also plotted the total number of individuals caught per total number of minutes of search time for each visit. I weighed and measured SVL (snout-vent length, 0.1 mm) with calipers for a maximum of 10 metamorphs per wetland per visit in 2008 and 2009.

Measurement of Environmental Features for Focal Wetlands

Because water temperature affects larval growth (Ultsch et al. 1999, Skelly et al. 2002), 10 of the 15 focal wetlands were intensively monitored in 2009. In four stormwater, three river valley, and three upland wetlands I placed two i-Button temperature loggers (iButton DS1921G#F50 - Maxim Integrated Products) and recorded temperature (Celsius) every 20 minutes from May 1 until July 29. At each wetland, one logger was placed at an egg-mass deposition site and the second was placed 5 m away in a random direction along the shore at an equal depth (~30 cm). Loggers were maintained at a depth of 30 cm and all vegetation near loggers was removed to prevent shading.

I examined the variability in water temperature between wetland types. It is possible that shallower wetlands, such as the upland wetlands in this study, display higher water temperatures than deeper stormwater wetlands because the sediment of shallow wetlands absorbs heat and subsequently releases heat back into the overlying water column. This re-radiation of heat can cause spiked water temperatures that may differ significantly from ambient air temperatures (Newman 1989, R.Vinebrooke, pers. com.). Considering this, hourly ambient air temperatures taken at the Municipal Airport in Edmonton from May 1 to July 29 were (acquired from Environment Canada, www.climate.weatheroffice.ec.gc.ca) compared to hourly water temperatures from each wetland.

In these same 10 wetlands on June 3, 2009, I placed two plastic plates (621.5 cm^2), one at each data logger location, to quantify periphyton production by measuring chlorophyll-*a*. Wood frog tadpoles have a diverse diet, but I chose to measure periphyton as a high quality food for larvae (Hocking and Semlitsch 2008, Purrenhage and Boone 2009). Plates were placed near the temperature loggers. I cleared submersed and emergent vegetation from the sites to prevent shading. Plates were collected on July 23rd. I scraped periphyton from the plates with a razor blade and placed samples on ice. Samples were analyzed using fluorometry by the Biogeochemical Analytical Laboratory at the University of Alberta within 24 hours of collection. I averaged chlorophyll-*a* concentrations from both plates for each site; all plates were lost at two upland wetlands and one river valley wetland.

STATISTICAL AND GIS ANALYSIS

Surveys

I summarized the occurrence of all species that were found at the three wetland types and used a G-test with a Williams' correction to compare boreal chorus frog and wood frog co-occurrence across all wetlands surveyed for calling adults.

All call, tadpole, and metamorph surveys were evaluated using descriptive statistics, graphs and tables to uncover trends. All results from statistical tests were considered significant at $\alpha = 0.05$. For 2008 and 2009, the largest chorus rank and overall estimate of total number of calling males recorded at each wetland was used to characterize the number of breeding males at each wetland. I also estimated the number of male frogs per BCS point by taking overall values, which were the total number of wood frogs heard calling per wetland and dividing by the total number of survey points. I conducted multiple surveys in 2009; therefore, I used the highest estimate of calling males from all surveys for each wetland. Overall estimates of calling male wood frog, highest call rank, and wood frogs per survey point were all highly correlated with each other for 2008 and 2009 (Range: $r_s = 0.643$ to 0.958 for all Spearman rank correlations, $n = 71$, $p < 0.001$). Therefore, I only report calling wood frogs per survey point for 2008 and 2009, instead of all three metrics. I compared estimates of male wood frogs per BCS point between 2008 and 2009 to identify whether there was consistency in the number of calling males between years. Because of a large number of zeros, the BCS data were heavily skewed to the left; I therefore, used non-parametric Spearman rank correlations to compare the two years (Luck et al. 2004). Data were not normal and lacked equal variance; therefore, I used a non-parametric Mann-Whitney U-test to compare differences in estimated number of males per survey point among stormwater, upland and river valley wetlands. Because amphibian behavior is largely influenced by precipitation, I compared 2008 and 2009 daily precipitation for three wetland locations.

Wetland Environmental Features

One-way ANOVAs were performed between wetland types, as well as between stormwater wetlands where wood frog was present versus absent for all 16 environmental features (Table 3.1 and Table 3.3). I did not conduct a multiple comparison correction (e.g., Bonferroni) because adjustment tests assume that multiple tests are all independent of one another and if the tests are not independent, the procedure may lead to higher probability of a Type II error (Gotelli and Ellison 2004). Additionally, multiple comparison tests assume that all of the null hypotheses are true (Gotelli and Ellison 2004). Data were natural log, $\log_{10}$, or square-root transformed to meet the assumptions of parametric tests (Sokal and Rohlf 1995). Data that did not meet assumptions after transformation were compared using a non-parametric single-factor Kruskal-Wallis test. Additionally, I used Non-Metric Multidimensional Scaling (NMDS; McCune and Grace 2002)) to construct a graphical representation of sample units (i.e., wetlands) in environmental space (i.e., 15 environmental parameters such as water chemistry, aquatic vegetation, and native vegetation surrounding each wetland). I chose NMDS as it is an ordination well suited for non-normal data and is considered the most effective ordination method for ecological data (McCune and Grace 2002). I used Bray-Curtis distance as my dissimilarity measure and a random starting configuration. The number of runs with real data and maximum number of iterations were set at 50 and 400, respectively. Prior to running ordinations, I used a correlation matrix to identify environmental variables that were redundant (i.e., variables with $r_s > 0.600$). All data were log transformed. Outlier analyses, with the cut-off set at two standard deviations, were also performed. A Monte Carlo test was used to test whether my final stress value could have been obtained by chance. All variables correlated with axis scores with $r^2 > 0.100$ were plotted as vectors with length representing the magnitude of this correlation. Vectors were considered highly correlated if they had an $r^2 > 0.500$. Multiple Response Permutation Procedures (MRPP) was used as a non-parametric test of differences in environmental data between the three wetland types (McCune & Grace 2002). I used Sorensen (Bray-Curtis) as my distance measure. The test statistic, *T*, indicates the separation of the groups, and the chance-corrected within-group agreement, *A*, reflects homogeneity within groups. NMDS and MRPP were performed with PC-ORD version 5 (MjM Software, Oregon, USA).

Role of Terrestrial Habitat

I tested for correlation among the nine land cover types around the 75 wetlands using Spearman rank correlation in SPSS (SPSS Inc., 2007). Highly correlated variables $r_s > 0.600$ were considered redundant and I therefore used one land cover type as representative of the other correlated cover types. Generalized linear logistic regression was used to relate the presence of calling male wood frogs in 2008 to the proportion of native habitat in concentric zones from 0-1000 m based on 10 m, 50 m, and 100 m intervals around all 75 BCS wetlands. I used 2008 BCS data because my imagery was from 2007. Because running multiple simultaneous regressions influences subsequent regressions, in the program R stats version 2.9.1 (R Project for Statistical Computing, http://www.r-project.org), I ran a single regression for wood frog occurrence for each zone resulting in a total of 130 regressions (100 regressions for 10 m intervals, 20 regressions for 50 m intervals, and 10 regressions for 100 m intervals). Models were evaluated using Akaike's Information Criterion adjusted for small samples (AIC_C) to identify the zone of terrestrial habitat (identified using 10m, 50m, and 100m intervals) within 0-1000 m of wetlands that best predicted wood frog occurrence. Attributes with an importance weight > 0.2 were considered substantial predictors of occurrence (Gahl and Calhoun 2008).

Abundance of Larvae and Metamorphs across Wetland Types

Stormwater wetlands are deeper than natural and river valley wetlands; therefore, much of their area is likely not used by tadpoles, which could cause densities to be underestimated. In order to derive accurate densities for tadpoles at stormwater wetlands, I estimated tadpole habitat as follows. Stormwater wetlands are constructed with a standardized 7:1 (horizontal:vertical) slope (Drainage Services, City of Edmonton, pers. comm.). I assumed that females do not deposit eggs in and tadpoles are not active in water greater than 1.5 m in depth. Therefore, I calculated the area of a zone extending 10.5 m out from the water's edge towards the center of each stormwater wetland to estimate available tadpole habitat. All densities for 2009 were based on the area of this zone. To be consistent between wetland types, I applied this same criterion to both upland and river valley wetlands.

I used simple linear regression to compare relative tadpole abundance to relative egg mass abundance, and relative egg mass density (derived by egg/area of 10.5 m zone) to relative tadpole density, in order to determine whether tadpole numbers were related to female breeding effort for 2008 (all 42 surveyed wetlands) and 2009 (13 focal wetlands). These relationships are important to consider because unequal breeding effort and/or egg mass mortality among wetland types could affect detection and abundances of tadpoles. Because achieving equal variance between wetland types was not possible, I used a non-parametric Mann-Whitney U-test to compare differences in tadpole relative abundances between wetland types for 2008 surveys. I compared 2009 tadpole and metamorph abundance between the three wetland types using a mixed linear model that accommodated a nested analysis of variance (ANOVA) in SPSS (SPSS Inc., 2007). This application allows fixed and random factors to be nested in a hierarchical order (see Hood and Bayley 2009). Each unique wetland was nested within wetland type. Wetland type was considered a fixed effect while wetland identity was treated as a random effect. Additionally, I accounted for temporal variation in data by including time (number of days since first survey) as a random effect.

Additionally, a univariate ANOVA was used to analyze differences in the size of emigrating metamorphs between two stormwater, one river valley, and one upland wetland. All comparisons were made by month (i.e., July, August, and September) based on pitfall trapping data from 2008. I only compared wetlands with more than 10 individuals for each month.

At the focal wetlands, I compared 2009 metamorph body size (i.e., SVL) between the three wetland types using a mixed linear model. Each unique wetland was nested within wetland type. Wetland type was considered a fixed effect while wetland identity was treated as a random effect. In order to address the possibility that I sampled the same individuals twice during repeated surveys, I re-ran the mixed linear model using two different data selection criteria: 1) I selected all data from one sampling date, with that date selected randomly for each wetland. and 2) I compared metmorph size from the first sampling dates from stormwater wetlands to metamorph size from the last sampling dates for river valley and upland wetlands. By using the latter selection criteria, I, in theory, compared the smallest (earliest sampled) frogs from stormwater wetlands to the largest (latest sampled) frogs from river valley and upland wetlands.

Using multiple linear regressions I compared average metamorph size to maximum water temperature, difference in maximum and minimum water temperatures, chlorophyll-a concentrations, wetland size, lead concentrations, submersed aquatic vegetation, total phosphorus, total nitrogen and larval density from the 15 focal wetlands sampled in 2009. All data were normal following a log transformation and all data were pooled, thus wetland type was not a factor in the analysis.

I used a univariate ANOVA to determine if the three types of wetlands displayed similar patterns in the conversion of eggs to larvae, I compared the ratio of tadpoles to egg mass numbers in 2008 for 18 wetland sites. These sites (eight upland, four river-valley, and six stormwater wetlands) had both eggs and tadpole data. Additionally, using a univariate ANOVA, I compared tadpole to egg and metamorph to tadpole ratios for the 13 focal wetlands sampled in 2009. In all aforementioned analyses, data were appropriately transformed to ensure normally distributed residuals.

Temperature at Focal Wetlands

I used daily temperature differences (maximum – minimum) to reflect the variability in temperature for each wetland. When comparing temperature among wetland types, I removed Wetland S/U308 from the stormwater category as it is a natural upland wetland that was incorporated into a stormwater system. Thus, S/U308 retained the bathymetric and hydrologic properties of an upland wetland and, therefore, likely has a thermal environment similar to other natural upland wetlands. S/U308 is considered a stormwater wetland for all other analyses.

Using Pearson's correlation I examined the association between daily maximum, minimum, and differences between maximum and minimum water to ambient air temperatures for each of the 10 wetlands that contained temperature loggers. This analysis allowed me to determine how strongly water temperatures responded to air temperature. I used a one-way ANOVA to test for differences in Pearson's coefficients between stormwater, river valley and upland wetlands. Differences in coefficient would suggest that one wetland type is more susceptible to deviation between water and ambient air temperatures and therefore may have a more dynamic within-wetland temperature regime. All temperature data were normally distributed.

RESULTS

Breeding Call Surveys

I found wood frog, boreal chorus frog and tiger salamander at all three wetland types. Boreal chorus frogs occurred at 45% of stormwater wetlands in 2008; however, the species was only present at 18% of stormwater wetlands in 2009. Boreal chorus frogs occurred at 83% of upland sites in 2008 and 2009, but less frequently at river valley wetlands, occurring at 60% of sites in 2008 and 40% in 2009. Although there were higher occurrences of chorus frog at both upland and river valley than stormwater wetlands, the number of calling males per survey point was greater at stormwater sites than at river valley wetlands (Table 3.4). Recorded during all BCS, egg, and metamorph surveys and as by-catch in minnow traps during tadpole surveys, tiger salamander occurred at 25% of upland, 60% of river valley and 10% of stormwater wetlands (Table 3.4). Neither Canadian toad or boreal toad was found at any of the 75 wetland sites.

However, individual male Canadian toads were located at three sites within one of the city's forested ravines. One of these toads was calling along a streamside pool, immediately adjacent to a river valley wetland site, the remaining two toads were calling along the same stream, but at locations with no adjacent wetlands.

Wood frog and boreal chorus frog co-occurred at 36 % of wetlands in 2008 and 28% in 2009 (Table 3.5a). A similar percentage of wetlands contained neither frog species; 27% in 2008 and 34% in 2009. The presence, absence and co-occurrence of both species were specific to wetland type. For example, 76% and 71% of all natural wetlands (upland and river valley) contained both wood frog and boreal chorus frog in 2008 and 2009, respectively. In contrast, in 2008, 19 of the 20 frog-less wetlands were stormwater and in 2009, 25 of 25 were stormwater wetlands. According to my goodness of fit test, co-occurrence of wood frog and boreal chorus frog did not significantly differ among all wetland sites (combined) in 2008 (Table 3.5b; G-test with Williams correction, $G = 0.380$, $df = 2$, $p\text{-value} = 0.8269$), however, co-occurrence did differ significantly among wetland sites in 2009 (G-test with Williams correction, $G = 33.601$, $df = 2$, $p\text{-value} < 0.001$). The difference in 2009 was likely a result of the substantial decrease in the occurrence of boreal chorus frog as the species disappeared from 17 wetland sites.

Wood Frog Breeding Call Surveys

In 2008 and 2009, calling wood frogs were heard at 57% and 63% of the 75 surveyed wetlands, respectively (Table 3.6). I detected calling frogs at 48% of stormwater wetlands in 2008 compared to 52% in 2009. Similar increases in the occurrence of calling frogs in 2009 were also noted in upland and river valley wetlands (Table 3.6). Precipitation was higher in 2008 than in 2009, thus many temporary wetland sites may have been dry or contained less water. This elimination of temporary breeding sites may have caused wood frogs to become concentrated at permanent stormwater wetland sites in 2009 (Fig. 3.3).

The number of calling wood frogs per survey point was more consistent between 2008 and 2009 (i.e., significantly correlated between years) at stormwater wetlands than at upland and river valley wetlands (Fig. 3.4). The average number of calling wood frogs per point was highest at upland wetlands and lowest at stormwater wetlands for both 2008 and 2009 (Table 3.6; upland > stormwater, Mann-Whitney U test, 2008: U = 133.5, p = 0.001, n = 68 and 2009: $U = 84.5$, $p < 0.001$, $n = 68$; upland ≈ river valley, Mann-Whitney U test, 2008: $U = 17.5$, $p = 0.187$, $n = 17$ and 2009: $U = 18$, $p = 0.234$, $n = 17$). The number of calling males per point at river valley wetlands did not differ from stormwater wetlands in 2008 (Mann-Whitney U test, $U = 91.5$, $p = 0.171$, $n = 61$), but were higher than stormwater wetlands in 2009 (Mann-Whitney U test, $U = 55$, $p = 0.02$, $n = 61$). However, after stormwater wetlands that lacked calling frogs were eliminated, the average number of wood frogs per point was similar to river valley wetlands in 2008 and 2009, but still lower than upland wetlands for both years (Table 3.6).

Wetland Environmental Features

Eight of 16 environmental features varied significantly among the three wetland types (Table 3.1). Four highly correlated variables were eliminated, and therefore, my ordination only included 11 of the total 15 variables (i.e., concentration of TP, chlorophyll-a, Zn, and Se were removed). Three upland wetlands were also excluded as outliers due to extremely high concentrations of contaminants Se, Pb, Cu, As, and Tn. My NMDS analysis yielded an optimum three-dimensional ordination space that collectively explained 91.2% of the variance (axis 1 = .356, axis 2 = 0.444, and axis 3 = 0.112) with an observed stress value of 7.724 and a stability of $<10^{-4}$ (McCune & Grace 2002). The strongest gradient across wetlands was due to wetland area and conductivity (Fig 3.5, $r = 0.5$) and to a lesser extent total nitrogen ($r = 0.4$). Stormwater wetlands were characterized by larger area than natural wetlands. The two axes showed a distinct clustering of sites based on wetland type (Fig. 3.5). Our MRPP analysis showed that the three wetland types differed in their overall environments (MRPP test, $T = -6.17$, $A = 0.07$, $P < 0.001$) and these differences were not due to chance (Monte Carlo test, $p = 0.01$). Pairwise comparisons indicated that upland and river valley wetlands were not different from each other in ordination space ($T = -0.76$, $A = 0.03$, $P = 0.198$), however, both differed significantly from stormwater wetlands (upland vs stormwater, $T = -7.55$, $A = 0.06$, $P < 0.001$; river valley vs. stormwater, $T = -2.17$, $A = 0.02$, $P = 0.04$).

I compared environmental variables between stormwater wetlands with and without wood frogs. Comparisons made by one-way ANOVAs indicated that year of construction and selenium were the only two variables of the 16 compared that significantly differed (with a p-value of 0.001) between stormwater wetlands with and without wood frogs (Table 3.3). Additionally, area, emergent vegetation, chlorophyll-a concentrations, and chromium differed significantly between stormwater wetlands with and without wood frogs (Table 3.3). Three highly correlated variables were eliminated, and therefore, my ordination only included 13 of the total 16 variables (TP, emerg, and pH were removed). NMDS analysis yielded a useful three-dimensional ordination space with an axis that explained 89.9% of the total variance with an observed stress value of 11.939 and a stability of $<10^{-4}$. Wetland area, chlorophyll-a, and conductivity were the only variables that were strongly correlated with axis scores (Fig 3.6, $r > 0.5$). Stormwater wetlands with and without frogs differed in their overall environments (MRPP test, $T = -5.13$, $A = 0.037$, $p = 0.001$). Overall, wood frogs were more likely to be present on smaller wetlands with lower conductivity and chlorophyll-a, and lower concentrations of nitrogen, selenium, copper, and chromium.

Terrestrial Habitat and Wood Frog Occurrence

Urban and native vegetation were the two dominant land-cover types in my study area, comprising 84% of the total landscape area (Table 3.7), and were negatively correlated with each other (Spearman rho $r = -0.782$, $n = 75$, $p < 0.001$). Native vegetation was also positively correlated with agriculture (Spearman rho $r = 0.438$, $n = 75$, $p < 0.001$) and negatively correlated with wetlands (Spearman rho $r = -0.329$, $n = 75$, $p < 0.004$).

There was a significant difference in the proportion of the surrounding area that was covered by native vegetation among the three wetland types (Table 3.1). River valley wetlands had the highest proportion (average of 92%) of native vegetation within the 0-100 m zone, which was expected as these wetlands are located within protected City of Edmonton parks. Land around stormwater wetlands supported the lowest proportions of native vegetation within 100 m with an average of 9% compared to 37% at upland wetlands. The occurrence of adult wood frog was best predicted by the amount of forest and shrubland habitat within spatial intervals nearest wetlands (Table 3.8). More specifically, the 0-10 m, 0-50m, and 0-100 m zones best predicted wood frog occurrence based on 10 m, 50 m and 100 m grain size, respectively (Table 3.8).

Egg Mass Surveys

In 2008, I found egg masses present at approximately 53% of all wetlands surveyed for eggs ($n = 43$). A higher percentage of upland and river valley wetlands had egg masses present, and natural wetlands had a higher average abundance of egg masses than stormwater wetlands (Table 3.6). However, for those wetlands with egg masses present (i.e., excluding all wetlands with eggs absent), stormwater wetlands had higher average egg mass abundance than river valley wetlands (Table 3.6). After accounting for those wetlands without eggs, egg densities (egg counts/wetland area) were two times higher at upland (0.02/m^2) versus river valley wetlands (0.01). and three times higher than stormwater wetlands (0.007). Egg mass abundances were positively correlated with the number of calling male frogs (Fig. 3.7, $R^2 = 0.567$, $df = 41$, $p < 0.001$). The focal wetlands surveyed in 2009 displayed a similar pattern, as natural and river valley wetlands contained more egg masses than stormwater wetlands (Table 3.9).

Tadpole Surveys

2008 tadpole surveys

In 2008, 64% of 39 wetlands with eggs had tadpoles present. The total tadpole occupancy was lower at stormwater wetlands compared to both river valley and upland wetlands, as less than half of stormwater sites had tadpoles present (Table 3.6). Upland and stormwater wetlands differed significantly in tadpole abundance (Mann-Whitney *U* test, $U = 34.0$, $p = 0.001$, $n = 35$), as did river valley and stormwater wetlands (Mann-Whitney *U* test, $U = 17.0$, $p = 0.029$, $n = 29$). Upland and river valley wetlands, however, did not differ in tadpole abundance (Mann-Whitney *U* test, $U = 11.0$, $p = 0.203$, $n = 14$). Tadpoles in upland wetlands were on average nine times more abundant (i.e., individuals per trap) than in river valley and 20 times more abundant than in stormwater wetlands. After excluding all wetlands that completely lacked tadpoles, larvae were 13 times more abundant in upland wetlands than either river valley or stormwater wetlands; however, tadpole abundance in river valley and stormwater wetlands were almost equal (Table 3.6). After excluding wetlands that lacked tadpoles, density (tadpole counts/wetland area) at upland wetlands (0.01/m^2) was 18 times higher and density at river valley wetlands (0.001/m^2) was two times higher than stormwater wetlands (0.0006/m^2).

In 2008, I sampled two stormwater and one upland wetland every two days between June 23 and 15 July to document tadpole growth. I caught more tadpoles at the upland (Wetland U410, N = 1305) versus either stormwater wetland (Wetland S403, N = 197; and Wetland S106, N = 23). Relative abundance (determined by total captures/ (number of minnow traps * number of survey days) was also higher at my upland wetland (12 tadpoles per trap-day) versus either stormwater wetlands (S403 = 2 tadpoles; S106 = 0.19 tadpoles).

2009 tadpole surveys

In 2009, tadpoles occurred at all focal wetlands, all of which also contained egg masses. The relative abundance of tadpoles (total number of tadpoles caught for all surveys/total number of dipnet attempts for all surveys) differed significantly across wetland types (Fig. 3.8, F = 4.261, df = 2, 112, $p < 0.001$; stormwater < river valley < upland). Tadpole abundances were 49 and 16 times higher at upland and river valley wetlands, respectively, than stormwater wetlands (Table 3.9). Likewise, average relative abundance for each sampling date was consistently higher at upland wetlands than river valley and stormwater wetlands across all surveys (Fig 3.8). Tadpole abundance was positively associated with female reproductive effort in 2009, as there was a significant linear relationship between relative tadpole abundance and egg mass number (Fig. 3.9, $R^2 = 0.646$, $df = 12$, $p = 0.001$). This trend was consistent with results from 2008 trapping, when tadpole relative abundances also increased with egg mass relative abundance, however, the relationship in 2008 was weaker ($R^2 = 0.128$, $df = 38$, $p = 0.007$). Similarly, tadpole density also increased with egg mass density at the 13 focal wetlands surveyed in 2009 (R^2 = 0.653, $df = 12$, $p < 0.001$). Tadpole density decreased with increased wetland area at these 13 sites ($R^2 = 0.516$, df =12, $p = 0.006$).

Metamorph Surveys

2008 metamorph surveys

Occurrence of metamorphs was lower at stormwater wetlands than at either river valley or upland wetlands (Table 3.6). However, metamorph surveys included all BCS wetlands in 2008, even those without calling males. After eliminating wetlands without adult frogs, frequency of occurrence increased as I detected metamorphs at 19% of stormwater wetlands in 2008.

2009 metamorph surveys

Occurrence was similar at upland and river valley wetlands in both years, however, frequency of occurrence increased at stormwater wetlands from 9% in 2008 to 30% in 2009. In 2009, metamorph relative abundance was higher at upland and river valley than stormwater wetlands (Fig 3.10, $F = 46.601$, $df = 2, 98$, $p < 0.001$). Metamorph relative abundance was 49 times higher at upland versus stormwater wetlands (Mann-Whitney U test, $U = 65.0$, $p = 0.002$, $n = 39$). Relative abundance at river valley wetlands was 14 times higher than at stormwater wetlands (Mann-Whitney U test, $U = 6.0$, $p = 0.001$, $n = 32$). When wetlands that completely lacked metamorphs were excluded, abundances in upland and river valley wetlands were 18 and 4 times higher than stormwater wetlands, respectively. Upland and stormwater wetlands differed significantly in metamorph abundance (Mann-Whitney U test, $U = 11.0$, $p = 0.027$, $n = 16$), but river valley and stormwater wetlands did not (Mann-Whitney U test, $U = 6.0$, $p = 0.089$, $n = 12$). At the focal wetlands sampled in 2009, metamorphs were present at all but two stormwater wetlands. Similar to the entire set of sites surveyed in 2009, metamorph relative abundance was 20 times higher at upland wetlands and 6 times higher at river valley wetlands than at stormwater wetlands.

Metamorph size among wetland types

In 2009, metamorphs were smallest at upland wetlands and largest at stormwater wetlands with significant differences existing between all three wetland types (Fig. 3.11, F = 31.424, df = 2, 208, $p < 0.001$; stormwater$_{(n = 6)}$ > upland$_{(n = 4)}$ < river valley$_{(n = 4)}$. After selecting all data from a date randomly chosen for each wetland, metamorphs were still smallest at upland wetlands and largest at stormwater wetlands (F = 19.403, df = 2, 83, p = 0.001). Additionally, metamorphs from the very first sampling period at stormwater wetlands were larger than metamorphs collected during the last surveys at river valley and upland wetlands (F = 13.411, df = 2, 85, p = 0.002). Overall, as density of tadpoles increased, metamorph body size decreased (R^2 = 0.801, df =11, $p < 0.001$).

Metamorph size and environmental features

For the focal wetlands, metamorph body size decreased with increased overall maximum temperatures (R^2 = 0.483, df =9, p = 0.026) and average difference between maximum and minimum temperatures in a 24 hour period (R^2 = 0.539, df =9, p = 0.016). Metamorph body size was negatively related to periphyton chlorophyll-a concentrations (R^2 = 0.729, df = 6, p = 0.014). Metamorph body size increased with increased wetland area (R^2 = 0.666, df = 11, p = 0.018) and increased lead concentrations (R^2 = 0.393, df = 11, p = 0.029). Metamorph size was not related to the proportion of submersed aquatic vegetation (R^2 = 0.206, df = 11, p = 0.161), total phosphorus concentration (R^2 = 0.216, df = 11, p = 0.128), or total nitrogen concentration (R^2 = 0.219, df = 11, p = 0.125).

Size of emigrating metamorphs

In 2008, metamorphs/young-of-the-year emigrating away from wetlands (caught via pitfall traps and drift fences from July to September) were heavier at the two stormwater wetlands versus the single upland wetland (Fig. 3.12). I did not catch emigrating metamorphs at river valley wetlands until September. Metamorphs at stormwater wetland S106 weighed significantly more than metamorphs at upland wetland U410 in July (Fig. 3.12, $S106_{n=59} > U410_{n=218}$; $F = 169.318$, $df = 1$, $p < 0.001$). This pattern also existed two months post-metamorphosis as young-of-the-year caught at drift fences were heavier at the two stormwater wetlands than at either natural wetland sites in both August and September,. This trend was statistically significant for August (Fig. 3.12, ($S106_{n=26}$, $S308_{n=15}$) > $U410_{n=21}$; $F = 27.448$, $df = 2$, $p < 0.001$). There were not enough individuals to statistically test size differences between stormwater and upland and river valley wetlands in September; however, the individuals caught at both stormwater wetlands were approximately 30-54% larger than those individuals found at either upland or river valley wetlands. Individuals were larger at upland than river valley wetlands in September ($RV315_{n=11} < U410_{n=212}$; $F = 12.689$, $df = 1$, $p < 0.001$).

Ratios of Eggs to Tadpole to Metamorph

The three types of wetlands displayed similar patterns in the conversion of eggs to larvae as the ratio of number of tadpoles to egg masses did not differ significantly among wetland types ($F = 1.428$, df =2, 17, $p = 0.271$) in 2008. When comparing this ratio at the subset of 13 wetlands in 2009, the ratio of tadpole density to egg mass density was highest at river valley and upland wetlands (tadpole density/egg mass density: upland = 0.018, river valley = 0.004, stormwater = 0.002); however, the ratio of metamorph density to tadpole density was highest at stormwater wetlands (upland = 3.9, river valley = 18.4, stormwater = 28.2).

Wetland Temperature at Focal Wetlands

The temperature difference (i.e., daily maximum minus minimum water temperatures) varied significantly between stormwater, river valley, and upland wetlands ($F = 46.897$, df =3, 859, $p < 0.001$; stormwater < rivervalley < upland < S/U308); however, after accounting for wetland as a random effect, temperature difference no longer varied significantly (Fig. 3.13, F = 2.618, df = 3, 859, p = 0.146). I compared maximum temperature, minimum temperature, and differences between maximum and minimum water temperatures to ambient air temperature. Maximum, minimum, and temperature differences in water were all significantly correlated to ambient air temperature for all wetland sites (Table 3.10). The strength of the correlation between water and air temperature, however, was significantly higher at stormwater and at river valley wetlands than at upland wetlands for maximum temperature and for the difference between maximum and minimum temperature (Table 3.10).

DISCUSSION

As urbanization steadily increases globally, there is a growing need to understand how habitat destruction and alteration from human activities not only affect amphibian distributions in urban landscapes, but other metrics such as relative abundance of individuals at various stages in their life cycle. If in this study, I had assessed the utility of stormwater wetlands for supporting frog populations solely based on adult presence, I likely would not have made an accurate assessment of their value in amphibian conservation. Although approximately 53% of wetlands had adult wood frogs present, many of these sites displayed no sign of recruitment of larvae or terrestrial juvenile life stages. Stage-specific responses to urbanization are not understood for most amphibian species as the majority of past urban studies have combined multiple stages into one measure, species occurrence (see Chapter 2). Monitoring of all age-classes is essential, as different life stages have specific habitat requirements and, therefore, respond differently to disturbances (Rothermel and Semlitsch 2002, Rothermel 2004, Lowe 2005). Hence, management of a species based on information derived from a single age class may be misguided (Rothermel and Semlitsch 2002).

Stormwater wetlands as habitat for amphibians

Although numerous studies suggest that urbanization negatively impacts amphibian communities and populations (Rubbo and Kiesecker 2005, Parris 2006, Gagné and Fahrig 2007), my results suggest that the creation of stormwater wetlands as well as the retention of natural wetlands within the urban matrix helps support adult urban wood frog, boreal chorus frog, and tiger salamander populations in Edmonton (for similar results in different geographic regions, see Colding et al. 2009, Simon et al. 2009). I found that stormwater wetlands were capable of accommodating the terrestrial life history phase (i.e., breeding adults) of wood frogs; although, stormwater wetlands had lower relative abundances of tadpoles and metamorphs when compared to both natural wetland types. Nonetheless, 30% of stormwater wetlands not only provided habitat for adult breeding, but also allowed recruitment (as indicated by the presence of metamorphs). This is surprising as wood frog is traditionally viewed as a forest-dependent species that is highly susceptible to urbanization (see Chapter 2).

In addition to services such as water storage and purification, stormwater wetlands can support frog populations and thus likely contribute to the preservation of local biodiversity. Accepting the current design and management of constructed wetlands as sufficient for the long-term management of urban frog populations, however should be done cautiously. More data that identify specific characteristics of stormwater wetlands that are or are not beneficial for populations is needed. For example, according to my NMS ordination, stormwater wetlands with and without wood frogs differed in their overall environments, with area having the most influence. In general, stormwater wetlands with wood frog presence were smaller, newer (i.e., post-1998), had less extreme water chemistry (e.g., lower total nitrogen concentrations, conductivity, and selenium) and more natural shorelines (i.e., contained more emergent vegetation). Therefore, depending on stormwater design, as well as within-pond parameters, some stormwater wetlands may not be able to support amphibian populations. Lastly, it is important to note that although all life-history stages were found at some stormwater wetlands, overall, stormwater wetlands are likely not as effective as natural urban wetlands for supporting self-sustaining wood frog populations.

Populations of many amphibian species associated with seasonal wetlands commonly experience wide variation in reproductive success between years (Taylor et al. 2006). For example in my study, because of lower precipitation in 2009 compared to 2008, two upland wetlands dried, which resulted in complete reproductive failure for wood frogs; however, these same wetlands had produced many metamorphs in 2008. Catastrophic year-class failures, caused by stochastic events such as drought, may cause fluctuations in amphibian populations and raise the thresholds of the level of survival of individuals required for persistence of populations (Taylor et al. 2006). Drought, however, is just one environmental variable that may affect amphibian populations. For example, there was a substantial decrease in male boreal chorus frog occurrence across all wetland sites from 2008 to 2009, however, this decrease was most pronounced at stormwater sites. Drought likely did not affect the hydrology of breeding sites, as stormwater wetlands are permanent; therefore, drought may have prevented movements of adults to and from breeding and overwintering sites. Alternatively, cold winter conditions and low snow cover may have caused mortality of adults prior to the spring breeding season. The former explanation seems less plausible as wood frog is equally susceptible to dry terrestrial conditions, yet this species' occurrence was more or less the same between 2008 and 2009.

Although I did not monitor wetland hydrology, upland and river valley wetlands have shallower maximum depths than stormwater wetlands and are more susceptible to early drying during drought years. Furthermore, natural wetlands located in urban landscapes may dry earlier because impervious surfaces impede ground water recharge (Brand and Snodgrass 2010). In addition to hydrological alteration, destruction of natural wetlands is prevalent in developed areas (e.g., approximately one out of every four upland wetlands in Edmonton was destroyed between 2001 and 2007, Scheffers unpublished data). Therefore, deeper permanent stormwater wetlands may be important in maintaining breeding habitat for amphibians during dry years and in compensating for natural wetland loss, assuming there is sufficient neighbouring terrestrial habitat for establishing and maintaining populations (Semlitsch 1998).

I recognize that permanent water bodies do have increased chances of fish colonization, which can adversely affect amphibian populations; however, recolonization by fish depends on geographic location as many permanent water bodies in my study region are fishless from winterkill events (Eaton et al. 2005). Although frog populations at stormwater wetlands seemed to have fewer breeding adults than natural wetlands (potentially a result of less surrounding terrestrial habitat within 100 m of wetland), almost half of the stormwater wetlands had adults present, thereby suggesting that stormwater wetlands can play an integral role in maintaining breeding populations in urban landscapes, particularly during drought years.

Adult wood frog occurrence and terrestrial habitat

Stormwater wetlands had smaller areas of native vegetation than upland and river valley wetlands and contained lower abundances of adults. The occurrence of wood frogs was best predicted by the proportion of native vegetation within 100 m of wetlands, a distance that corresponds to post-breeding movements of wood frog in eastern North America (Rittenhouse and Semlitsch 2007a). Limited landscape connectivity caused by terrestrial habitat loss hampers dispersal and migration, two processes essential to individual and population persistence

(Semlitsch 2008). For amphibians with dual habitat requirements, both adult and recently metamorphosed juveniles, commonly direct their movements towards native habitat, particularly areas with greater forest cover (Homan et al. 2008, Walston and Mullin 2008). Similarly, I observed that wood frogs would not move through urbanized landscapes, whereas individuals readily moved through forest habitats in my study area (BRS unpublished data). Therefore, without stormwater wetlands that are connected to suitable terrestrial habitat to allow for movements at a landscape scale, the majority of animals may remain in local habitat patches (e.g., the immediate riparian zone around wetlands), as successful movements through large expanses of dry inhospitable habitat are unlikely.

Previous work on body size and movements in northern red-legged frog (*Rana aurora*) and wood frog suggest that larger individuals (both juveniles and adults) can move further and are more resilient to desiccation in disturbed environments than smaller individuals (Mazerolle 2001, Chelgren et al. 2006). Although metamorphs from stormwater wetlands are larger on average than animals from natural wetland systems, whether or not these size differences confer advantages in hostile urban environments is unknown. Small amphibians lose water faster than larger individuals of the same species (Thorson 1955, Ray 1958, Spight 1968); therefore, larger individuals should be better equipped to move within drier habitats such as urban landscapes. For example, wood frogs that occurred in forest fragments were consistently larger than those found in continuous forest habitat (Mazerolle 2001). Similarly, initial emigration movements of newly metamorphosed northern red-legged frogs (*Rana aurora aurora*), usually traveling distances of 12 to 40 m from breeding wetlands, are about one to two times more likely to survive and emigrate with each 1 mm increase in snout-vent length (Chelgren et al 2006). In my study, metamorphs from stormwater sites were on average 7 mm larger than those from upland wetlands, thus, if increased size results in greater survival during emigration, stormwater metamorphs may be better suited to withstand dry urban environments (Mazerolle 2001). However, an accurate estimate of survival during emigration must account for additional factors that may increase mortality in urban environments such as increased number of roads (Fahrig and Rytwinski 2009).

The colonization of stormwater wetlands could occur by chance dispersals through urban landscapes; however, maintaining wood frog populations from year to year likely requires sufficient suitable habitat immediately surrounding (e.g., within 164 m) wetlands for overwintering (Semlitsch 1998). My analyses suggest that wood frog presence is best predicted by the amount of native vegetation at both very local (0-10 m) and slightly larger scales (50-100 m and 0-100 m) surrounding urban wetlands. Very local vegetation was likely most influential in determining the presence of wood frog as this area corresponds to the 5-25 m riparian zone, typically consisting of tall grass that is often left at urban wetlands in Edmonton. Retaining native vegetation immediately adjacent to stormwater wetlands likely provides enough habitat to maintain small wood frog populations; however, as long as native habitat remains limited at both the local and overall landscape scale (i.e., up to 1000 m), populations will remain small or absent at stormwater wetlands with high risks of local extinction and low likelihoods of colonization (Burbrink et al. 1998, Semltisch 2008). Population persistence also depends on the relationship between the areas of breeding and terrestrial habitats, as the size of adult wood frog populations was significantly correlated with the size of the larval habitat at numerous wetlands in Michigan, USA (Benard et al. 2009). Thus, the interplay of the quality of habitat offered by stormwater wetlands and by adjacent terrestrial habitat may be critical in determining the size, structure and persistence of wood frog populations.

Wood frog life-history stages at stormwater wetlands

With a few exceptions (e.g., Brand and Snodgrass 2010), ecologists have not considered whether frog populations at stormwater wetlands are capable of recruitment to terrestrial life stages, and how various attributes of frog life-history stages compare between stormwater and natural wetlands. Indicators of poor performances of stormwater wetlands as breeding habitat for wood frogs, compared to natural wetlands, could include both the relatively rare occurrence of larval and metamorph life stages accompanied by small body size and poor condition of surviving metamorphs. Although stormwater wetlands seem to attract fewer breeding females and males, decreased tadpole density at stormwater wetlands may have contributed to the production of significantly larger metamorphs (see Scott 1994 and Loman 2004 for examples of density dependent growth in larvae). It is important to note that this trend could also be caused by equal numbers of breeding adults, but poorer survivorship of eggs and hatchlings. However, we found overall lower breeding effort at stormwater wetlands.

In 2009, metamorph body size was 28% and 18% larger at stormwater wetlands than in natural and river valley wetlands, respectively. Similar trends were observed for metamorphs emigrating in 2008, as the average mass of metamorphs was approximately 44% heavier in July and 37% heavier in September at stormwater compared to upland wetlands. Whether or not these size differences are beneficial to individuals that eventually breed in stormwater systems remains undetermined. However, studies of the salamander *A. opacum* (marbled salamander) in Georgia and the frog *P. triseriata* (western chorus frog) in Michigan, USA suggest body size differences between 9 and 18% , respectively can lead to greater recruitment of individuals into juvenile life-history stages and increased survivorship to maturity (Smith 1987, Scott 1990). My preliminary assessment suggests larger body size in stormwater metamorphs could translate into increased survival (Goater 1994), if suitable terrestrial habitat is available to support terrestrial life stages (Houlahan and Findlay 2003, Browne et al. 2009). Insufficient terrestrial habitat is potentially one explanation for why wood frog populations at stormwater wetlands remain low, despite the production of larger metamorphs.

Larval density plays an important role in population regulation in both the aquatic and terrestrial life stages (Scott 1994). Larvae of various amphibian species such as wood frog, eastern spadefoot toad (*Scaphiopus holbrookii*) and marbled salamander reared under low densities are often larger as juveniles and adults, younger at first reproduction (Semlitsch and Caldwell 1982, Berven 1990, Scott 1994), and display increased survival for terrestrial life stages (Berven 1990, Goater 1994). In short, growth and size at the tadpole and metamorph stage may have population-level impacts that are not expressed until later life stages (Berven 1990, Chelgren et al. 2006). Size may affect aerobic performance (Goater et al. 1993) as well as a frog's ability to forage, overwinter and escape predators (Chelgren et al. 2006). Larger body size of metamorphs immediately prior to overwintering may also be particularly important for withstanding low winter temperatures representative of the study region (Boone 2005). More research is needed to fully prove long-term advantages of large body size and whether urban frog populations are regulated by adult and/or tadpole life-history stages, particularly in landscapes where both aquatic and terrestrial habitats are commonly man-made and/or manipulated.

Mechanisms for body sizes differences between wetland types

In this study, I focused on comparing metamorph size between stormwater and natural wetlands rather than a comprehensive evaluation of specific causal factors behind size differences. Nevertheless, I identified several potential mechanisms, such as maximum water temperature and high tadpole density, that were all negatively correlated with body size at metamorphosis. My results suggest that in upland wetlands with high larval densities and highly fluctuating temperature regimes, metamorphs are smaller bodied even though these systems have higher chlorophyll-a concentrations (Govindarajulu and Anholt 2006). Stress endured during chronic intermittent exposure to high temperatures (e.g., approaching 40°C as found in this study) that surpass the optimal temperature range or refect large variation in daily temperature may suppress growth of tadpoles in upland wetlands and result in small body size at metamorphosis (Ultsch et al. 1999, Bevelhimer and Bennett 2000, Maciel and Juncá 2009).

Two prior studies found wood frogs critical thermal maximum (temperature at which locomotor activity becomes impaired and the animals loses its ability to escape hostile/lethal conditions) to be around 37.9 - 39.6 °C (Cupp 1980 and Manis and Claussen 1986). In my study, deeper, large stormwater wetlands, which on average, contained cooler and less variable thermal conditions may therefore provide a temperature gradient with depth for buffering high temperatures (Newman 1989). More research is needed to better understand the role of high water temperature or the combination of high water temperature and high larval densities in suppressing larval growth in stormwater and natural wetlands. For example, river valley wetlands had water temperatures similar to stormwater wetlands, yet metamorph size differed between the two wetland types. Additionally, although wetland S/U308 (a natural upland wetland incorporated in stormwater management) displayed temperatures similar to upland wetlands, larval density and metamorph size were comparable to stormwater wetlands.

There are many other factors that influence size at metamorphosis, which include wetland area, predation, parasitism, and/or disease (Pearman 1993, Werner and Anholt 1996, Berven and Boltz 2001). Focal stormwater wetlands in my study were much larger in size and deeper than natural wetlands. Increased area and depth of aquatic habitat led to lower survival, but greater growth in *Lithobates clamitans* (green frog) larvae (Pearman 1993). I found similar trends at my focal wetland sites as metamorph size increased with wetland area; however, this may be an indirect result of a strong relationship between tadpole density and wetland area.

According to my ANOVA comparisons, both total nitrogen and total phosphorus significantly differed among wetland types. Upland wetlands tended to have higher total nitrogen than the other two wetland types; however, the strongest gradient across wetlands (according to NMS ordination) reflects wetland area and conductivity. The effects of elevated nitrogen on larvae is uncertain, for example, Massal et al. (2007) found no association between high nitrogen level (e.g., nitrogen pollution) and occurrence of six amphibian species at stormwater wetlands, whereas Earl and Whiteman (2009) found that relatively low doses of nitrate may adversely affect larvae development of *Hyla chrysoscelis*. Although hypereutrophic conditions naturally occur in upland wetlands within my study area (Anderson et al. 2002), the lower nitrogen levels at stormwater compared to upland wetlands may contribute to a more suitable environment for tadpole development. Fewer tadpoles therefore at stormwater wetlands are likely due to fewer breeding adults as I found a strong linear relationship between female egg masses and relative abundances of tadpoles across all wetland sites.

High metal concentrations at upland wetlands may be attributed to both point and non-point source pollution as all natural wetlands in my study area were located within an urbanized watershed. Although metamorph size decreased with increased lead concentrations, this relationship may be coincidentally attributed to the seasonal hydrology of upland wetlands, which likely increased metal and nutrient concentrations as water levels drop.

Density dependent growth in terrestrial urban environments

Density dependent growth and survival also affects the terrestrial stage of amphibians in natural environments. Harper and Semlitsch (2007) found that juvenile density in the terrestrial stage can negatively affect growth, survival and stage of reproductive development of wood frog. Similarly, increased density of adults can adversely affect the growth of other adults in some amphibian species (Loman and Lardner 2009). Assessing whether density dependent growth and survival is more prominent in the aquatic or terrestrial life stages in urban environments, therefore, deserves further exploration and discussion. For example, metamorphs at upland and river valley wetlands were smaller-bodied and were many times more abundant and dense than at stormwater wetlands. At the same time, many of the upland and river valley wetlands contained more terrestrial habitat and, therefore, metamorphs likely occurred at lower densities after dispersing to the terrestrial environment. The size advantage gained by metamorphs emerging from stormwater wetlands, combined with low metamorph abundances, may translate into additional advantages (i.e., large body size and low terrestrial densities as juveniles and adults) for these individuals during terrestrial life-history stages. This advantage assumes that suitable terrestrial habitat is maintained adjacent to stormwater wetlands. Without sufficient areas of intact and connected terrestrial habitat, these size advantages are irrelevant at terrestrial life stages as individuals may choose to live at high densities in high-quality habitat (e.g., patch of forest), rather than occupy low-quality habitat at lower densities (e.g., manicured lawn) (Patrick et al. 2008).

Urban amphibian conservation

For effective amphibian conservation, preserving terrestrial habitat should have precedence over allocating resources for the formulation of complex wetland design, as wood frogs do breed in and seem to recruit successfully individuals from stormwater wetlands.

However, it should be remembered that upland and river valley wetlands had higher occurrence and abundance of wood frog than stormwater wetlands. Urban land is both limited and expensive, therefore focusing on the terrestrial habitat needs of adult frogs would likely best serve management objectives aimed at maintaining viable populations in urban environments rather than purchasing wetland habitat. I do not advocate the abandonment of wetland habitat preservation, but instead there should be a compromise between natural wetland and terrestrial habitat preservation. Future research should investigate various stormwater designs for supporting populations of multiple species of amphibians. Although I found two other amphibian species present at stormwater wetlands, more research is needed to assess whether other pond-breeding species are capable of recruiting individuals from stormwater sites. Habitat loss is the most ubiquitous force driving amphibian decline and extinction globally (Sodhi et al. 2008); however, in the context of urban landscapes, where the creation of water retention facilities is already required for flood prevention, focusing on preserving native terrestrial habitat is likely most essential in maintaining amphibian populations.

LITERATURE CITED

Abbasi, S. A., V. Baji, and R. Soni. 1989. Assessment of the impact of simulated acid rain and alkaline effluent discharge on pond biota with respect to larvae of Amphibian Rana tigrina. International Journal of Environmental Studies **35**:97-103.

Adams, M. J. 2000. Pond permanence and the effects of exotic vertebrates on anurans. Ecological Applications **10**:559-568.

Alberta Environmental Protection. 1997. The parkland natural region of Alberta. Alberta Government, Edmonton, AB. 111 pp

AmphibiaWeb: Information on amphibian biology and conservation. [web application]. 2009. Berkeley, California: AmphibiaWeb. Available: http://amphibiaweb.org/.

Anderson, A., G. Byrtus, J. Thompson, D. Humphries, B. Hill, and M. Bilyk. 2002. Baseline pesticide data for semi-permanent wetlands in the aspen parkland of Alberta. Alberta Environment, Pub No. T/673. Edmonton, Alberta, Canada.

Battin, J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. Conservation Biology **18**:1482-1491.

Bayley, S. E. and C. M. Prather. 2003. Do wetland lakes exhibit alternative stable states? Submersed aquatic vegetation and chlorophyll in western boreal shallow lakes. Limnology and Oceanography **48**:2335-2345.

Benard, M. F., E. E. Werner, R. A. Relyea, D. K. Skelly, K. L. Yurewicz. 2009. At which life-stage are amphibian populations regulated? A test with wood frogs. 94th Annual Meeting of the Ecological Society of America.

Berven, K. A. and R. S. Boltz. 2001. Interactive effects of leech (*Desserobdella picta*) infection on wood frog (*Rana sylvatica*) tadpole fitness traits. Copeia **2001**:907-915.

Berven, K. A. and T. A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): Implications for genetic population structure. Evolution **44**:2047-2056.

Bevelhimer, M. and W. Bennett. 2000. Assessing cumulative thermal stress in fish during chronic intermittent exposure to high temperatures. Environmental Science and Policy **3**: 211-216.

Bhamidimarri, R., A. Shilton, I. Armstrong, P. Jacobson, and D. Scarlet. 1991. Constructed wetlands for waster-water treatment: The New Zealand experience. Water Science and Technology **24**:247-253.

Boone, M. D. 2005. Juvenile frogs compensate for small metamorph size with terrestrial growth: Overcoming the effects of larval density and insecticide exposure. Journal of Herpetology **39**:416-423.

Bowles, B. D., M. S. Sanders, and R. S. Hansen. 2006. Ecology of the Jollyville Plateau salamander (*Eurycea tonkawae* : Plethodontidae) with an assessment of the potential effects of urbanization. Hydrobiologia **553**:111-120.

Brand, A. B. and J. W. Snodgrass. 2010. Value of artificial haibtats for amphibian reproduction in altered landscapes. Conservation Biology **24**: 295-301.

Brix, H. 1995. Use of constructed wetlands in water-pollution control: Historical development, present status, and future perspectives. Water Science and Technology **30:**209-223.

Browne, C. L., C. A. Paszkowski, A. L. Foote, A. Moenting, and S. M. Boss. 2009. The relationship of amphibian abundance to habitat features across spatial scales in the Boreal Plains. Ecoscience **16**:209-223.

Burbrink, F. T., C. A. Phillips, and E. J. Heske. 1998. A riparian zone in southern Illinois as a potential dispersal corridor for reptiles and amphibians. Biological Conservation **86**:107-115.

Camargo, J. A., A. Alonso, and A. Salamanca. 2005. Nitrate toxicity to aquatic animals: a review with new data for freshwater invertebrates. Chemosphere **58**:1255-1267.

Camponelli, K. M., R. E. Casey, J. W. Snodgrass, S. M. Lev, and E. R. Landa. 2009. Impacts of weathered tire debris on the development of *Rana sylvatica* larvae. Chemosphere **74**:717-722.

Chelgren, N. D., D. K. Rosenberg, S. S. Heppell, and A. I. Gitelman. 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. Ecological Applications **16**:250-261.

Colding, J., J. Lundberg, S. Lundberg, and E. Andersson. 2009. Golf courses and wetland fauna. Ecological Applications **19**:1481-1491.

Crouch, W. B. and P. W. C. Paton. 2000. Using egg-mass counts to monitor wood frog populations. Wildlife Society Bulletin **28**:895-901.

Cupp, P. V. Jr. 1980. Thermal tolerance of five salientian amphibians during development and metamorphosis. Herpetologica **36**:234-244.

Danylchuk, A. J. and W. M. Tonn. 2003. Natural disturbances and fish: Local and regional influences on winterkill of fathead minnows in boreal lakes. Transactions of the American Fisheries Society **132**:289-298.

Earl, J. E. and H. H. Whiteman. 2009. Effects of pulsed nitrate exposure on amphibian development. Environmental Toxicology and Chemistry **28**:1331-1337.

Eaton, B. R., W. M. Tonn, C. A. Paszkowski, A. J. Danylchuk, and S. M. Boss. 2005. Indirect effects of fish winterkills on amphibian populations in boreal lakes. Canadian Journal of Zoology-Revue Canadienne De Zoologie **83**:1532-1539.

Egan, R. S. and P. W. C. Paton. 2004. Within-pond parameters affecting oviposition by wood frogs and spotted salamanders. Wetlands **24**:1-13.

Fahrig, L. and T. Rytwinski. 2009. Effects of Roads on Animal Abundance: an Empirical Review and Synthesis. Ecology and Society **14**:21.

Gagne, S. A. and L. Fahrig. 2007. Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada. Landscape Ecology **22**:205-215.

Gahl, M. K. and A. J. K. Calhoun. 2008. Landscape setting and risk of Ranavirus mortality events. Biological Conservation **141**:2679-2689.

Gibbs, J. P., K. K. Whiteleather, and F. W. Schueler. 2005. Changes in frog and, toad populations over 30 years in New York State. Ecological Applications **15**:1148-1157.

Goater, C. P. 1994. Growth and survival of postmetamorphic toads – interactions among larval history, density, and parasitism. Ecology **75**:2264-2274.

Goater, C. P., R. D. Semlitsch, and M. V. Bernasconi. 1993. Effects of body size and parasite infection on the locomotory performance of juvenile toads, *Bufo bufo*. Oikos **66**:129-136.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica **16**:183-190.

Gotelli, N. J. and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Inc. Sunderland, Massachusetts, U.S.A.

Govindarajulu, P. P. and B. R. Anholt. 2006. Interaction between biotic and abiotic factors determines tadpole survival rate under natural conditions. Ecoscience **13**:413-421.

Hamer, A. J. and M. J. McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: A review. Biological Conservation **141**:2432-2449.

Harper, E. B. and R. D. Semlitsch. 2007. Density dependence in the terrestrial life history stage of two anurans. Oecologia **153**:879-889.

Hocking, D. J. and R. D. Semlitsch. 2008. Effects of Experimental Clearcut Logging on Gray Treefrog (*Hyla versicolor*) Tadpole Performance. Journal of Herpetology **42**:689-698.

Homan, R. N., C. D. Wright, G. L. White, L. F. Michael, B. S. Slaby, and S. A. Edwards. 2008. Multiyear Study of the Migration Orientation of *Ambystoma maculatum* (Spotted Salamanders) among Varying Terrestrial Habitats. Journal of Herpetology **42**:600-607.

Hood, G. A. and S. E. Bayley. 2009. A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. Forest Ecology and Management **258**:1979-1989.

Hopkins, W. A., J. Congdon, and J. K. Ray. 2000. Incidence and impact of axial malformations in larval bullfrogs (*Rana catesbeiana*) developing in sites polluted by a coal-burning power plant. Environmental Toxicology and Chemistry **19**:862-868.

Horne, M. T. and W. A. Dunson. 1995. Effects of low pH, metals and water hardness on larval amphibians. Archives of Environmental Contamination and Toxicology **29**:500-505.

Houlahan, J. E. and C. S. Findlay. 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences **60**:1078-1094.

Lehtinen, R. M., S. M. Galatowitsch, and J. R. Tester. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands **19**:1-12.

Loman, J. and B. Lardner. 2009. Does landscape and habitat limit the frogs *Rana arvalis* and *Rana temporaria* in agricultural landscapes? A field experiment. Applied Herpetology **6**:227-236.

Lowe, W. H. 2005. Factors affecting stage-specific distribution in the stream salamander *Gyrinophilus porphyriticus*. Herpetologica **61**:135-144.

Luck, G. W., T. H. Ricketts, G. C. Daily, and M. Imhoff. 2004. Alleviating spatial conflict between people and biodiversity. Proceedings of the National Academy of Sciences of the United States of America **101**:182-186.

Maciel, T. A., and F. A. Juncá. 2009. Effects of temperature and volume of water on the growth and development of tadpoles of *Pleurodema diplolister* and *Rhinella granulose* (Amphibia: Anura). Zoologia **26**:413-418.

Manis, M. L., and D. L. Claussen. 1986. Environmental and genetic influences on the thermal physiology of Rana sylvatica. Journal of Thermal Biology **11**:31-36.

Massal, L. R., J. W. Snodgrass, and R. E. Casey. 2007. Nitrogen pollution of stormwater ponds: Potential for toxic effects on amphibian embryos and larvae. Applied Herpetology **4**:19-29.

Mazerolle, M. J. 2001. Amphibian activity, movement patterns, and body size in fragmented peat bogs. Journal of Herpetology **35**:13-20.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. Bioscience **52**:883-890.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation **127**:247-260.

Newman, R. A. 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology **70**:1775-1787.

Newman, R. A. 1998. Ecological constraints on amphibian metamorphosis: interactions of temperature and larval density with responses to changing food level. Oecologia **115**:9-16.

Ostergaard, E.C., Richter, K.O., West, S.D., 2008. Amphibian use of stormwater ponds in the Puget Lowlands of Washington, USA. In: Mitchell, J.C., Jung Brown, R.E., and Bartholomew, B., (Eds.), Urban Herpetology. Society for the Study of Amphibians and Reptiles, Salt Lake City, U.S.A., pp. 259-270.

Parris, K. M. 2006. Urban amphibian assemblages as metacommunities. Journal of Animal Ecology **75**:757-764.

Patrick, D. A., E. B. Harper, M. L. Hunter, Jr., and A. J. K. Calhoun. 2008. Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. Ecology **89**:2563-2574.

Pearl, C. A., M. J. Adams, N. Leuthold, and R. B. Bury. 2005. Amphibian occurrence and aquatic invaders in a changing landscape: Implications for wetland mitigation in the Willamette Valley, Oregon, USA. Wetlands **25**:76-88.

Pearman, P. B. 1993. Effects of habitat size on tadpole populations. Ecology **74**:1982-1991.

Pellet, J., A. Guisan, and N. Perrin. 2004. A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. Conservation Biology **18**:1599-1606.

Purrenhage, J. L. and M. D. Boone. 2009. Amphibian community response to variation in habitat structure and competitor density. Herpetologica **65**:14-30.

R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raimondo, S. M., C. L. Rowe, and J. D. Congdon. 1998. Exposure to coal ash impacts swimming performance and predator avoidance in larval bullfrogs (*Rana catesbeiana*). Journal of Herpetology **32**:289-292.

Ray, C. 1958. Vital limits and rates of desiccation in salamanders. Ecology **39**:75-83.

Riley, S. P. D., G. T. Busteed, L. B. Kats, T. L. Vandergon, L. F. S. Lee, R. G. Dagit, J. L. Kerby, R. N. Fisher, and R. M. Sauvajot. 2005. Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. Conservation Biology **19**:1894-1907.

Rittenhouse, T. A. G. and R. D. Semlitsch. 2007a. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands **27**:153-161.

Rittenhouse, T. A. G. and R. D. Semlitsch. 2007b. Postbreeding habitat use of wood frogs in a Missouri oak-hickory forest. Journal of Herpetology **41**:645-653.

Rothermel, B. B. 2004. Migratory success of juveniles: A potential constraint on connectivity for pond-breeding amphibians. Ecological Applications **14**:1535-1546.

Rothermel, B. B. and R. D. Semlitsch. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology **16**:1324-1332.

Rouse, J. D., C. A. Bishop, and J. Struger. 1999. Nitrogen pollution: An assessment of its threat to amphibian survival. Environmental Health Perspectives **107**:799-803.

Royer F. and R. Dickinson. 2007. Plants of Alberta: Trees, shrubs, wildflowers, ferns, aquatic plants and grasses. Lone Pine Publishing, Edmonton, Canada.

Rubbo, M. J. and J. M. Kiesecker. 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology **19**:504-511.

Russell, A. P. and A. M. Bauer. 2000. The amphibians and reptiles of Alberta: A field guide and primer of boreal herpetology. University of Calgary Press. Calgary, Canada.

Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: An experiment in large-scale field enclosures. Ecology **71**:296-306.

Scott, D. E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology **75**:1383-1396.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology **12**:1113-1119.

Semlitsch, R. D. and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology **17**:1219-1228.

Semlitsch, R. D. and J. P. Caldwell. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrookii*. Ecology **63**:905-911.

Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*.. Ecology **69**:184-192.

Sharma, B. and R. Patiño. 2009. Effects of cadmium on growth, metamorphosis and gonadal sex differentiation in tadpoles of the African clawed frog, *Xenopus laevis*. Chemosphere **76**:1048-1055.

Shirose, L. J., C. A. Bishop, D. M. Green, C. J. MacDonald, R. J. Brooks, and N. J. Helferty. 1997. Validation tests of an amphibian call count survey technique in Ontario, Canada. Herpetologica **53**:312-320.

Simon, J. A., J. W. Snodgrass, R. E. Casey, and D. W. Sparling. 2009. Spatial correlates of amphibian use of constructed wetlands in an urban landscape. Landscape Ecology **24**:361-373.

Skelly, D. K., L. K. Freidenburg, and J. M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. Ecology **83**:983-992.

Skidds, D. E., F. C. Golet, P. W. C. Paton, and J. C. Mitchell. 2007. Habitat correlates of reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed. Journal of Herpetology **41**:439-450.

Smith, B. R. 2009. Re-thinking wastewater landscapes: combining innovative strategies to address tomorrow's urban wastewater treatment challenges. Water Science and Technology **60**:1465-1473.

Smith, D. C. 1987. Adult recruitment in chorus frogs-effects of size and date at metamorphosis. Ecology **68**:344-350.

Smith, M.A and D.M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography **28**: 110-128.

Snodgrass, J. W., R. E. Casey, D. Joseph, and J. A. Simon. 2008. Microcosm investigations of stormwater pond sediment toxicity to embryonic and larval amphibians: Variation in sensitivity among species. Environmental Pollution **154**:291-297.

Sodhi, N., D. Bickford, A. Diesmos, T. Lee, L. Koh, B. W. Brook, C. Sekercioglu, and C. J. A. Bradshaw. 2008. Measuring the meltdown: Drivers of global amphibian extinction and decline. PLoS ONE **3**:e1636. doi:1610.1371/journal.pone.0001636.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry. W. H. Freeman, New York.

Spight, T. M. 1968. Water economy of salamanders-evaporative water loss. Physiological Zoology **41**:195-203.

Spss Inc. 2003. SPSS for Windows, Release 12.0.0. SPSS Inc., Chicago, IL.

Stevens, C. E. and C. A. Paszkowski. 2004. Using chorus-size ranks from call surveys to estimate reproductive activity of the wood frog (*Rana sylvatica*). Journal of Herpetology **38**:404-410.

Stewart, Robert E., and Harold A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Resource Publication 92, Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service, Washington, D.C. Jamestown, ND: Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/wetlands/pondlake/index.htm (Version 16APR1998).

Taylor, B. E., D. E. Scott, and J. W. Gibbons. 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation Biology **20**:792-801.

Thorson, T. B. 1955. The relationship of water economy to terrestrialism in amphibians. Ecology **36**:100-116.

Ultsch, G. R., D. F. Bradford, and J. Freda. 1999. Physiology: Coping with the environment. In: McDiarmid, R. W. and R. Altig. (Eds.), Tadpoles: The biology of anuran larvae. The University of Chicago Press, Chicago, U.S.A., pp. 189.

Walston, L. J. and S. J. Mullin. 2008. Variation in amount of surrounding forest habitat influences the initial orientation of juvenile amphibians emigrating from breeding ponds. Canadian Journal of Zoology-Revue Canadienne De Zoologie **86**:141-146.

Wiens, J. A., 1989. Spatial scaling in ecology. Functional Ecology **3**: 385-397.

Weir, L. 2001. Voices in the night: A calling frog survey. Wild Earth **11**:44-45.

Werner, E. E. and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: Consequences to competitive interactions in anuran larvae. Ecology **77**:157-169.

Woodford, J. E. and M. W. Meyer. 2003. Impact of lakeshore development on green frog abundance. Biological Conservation **110**:277-284.

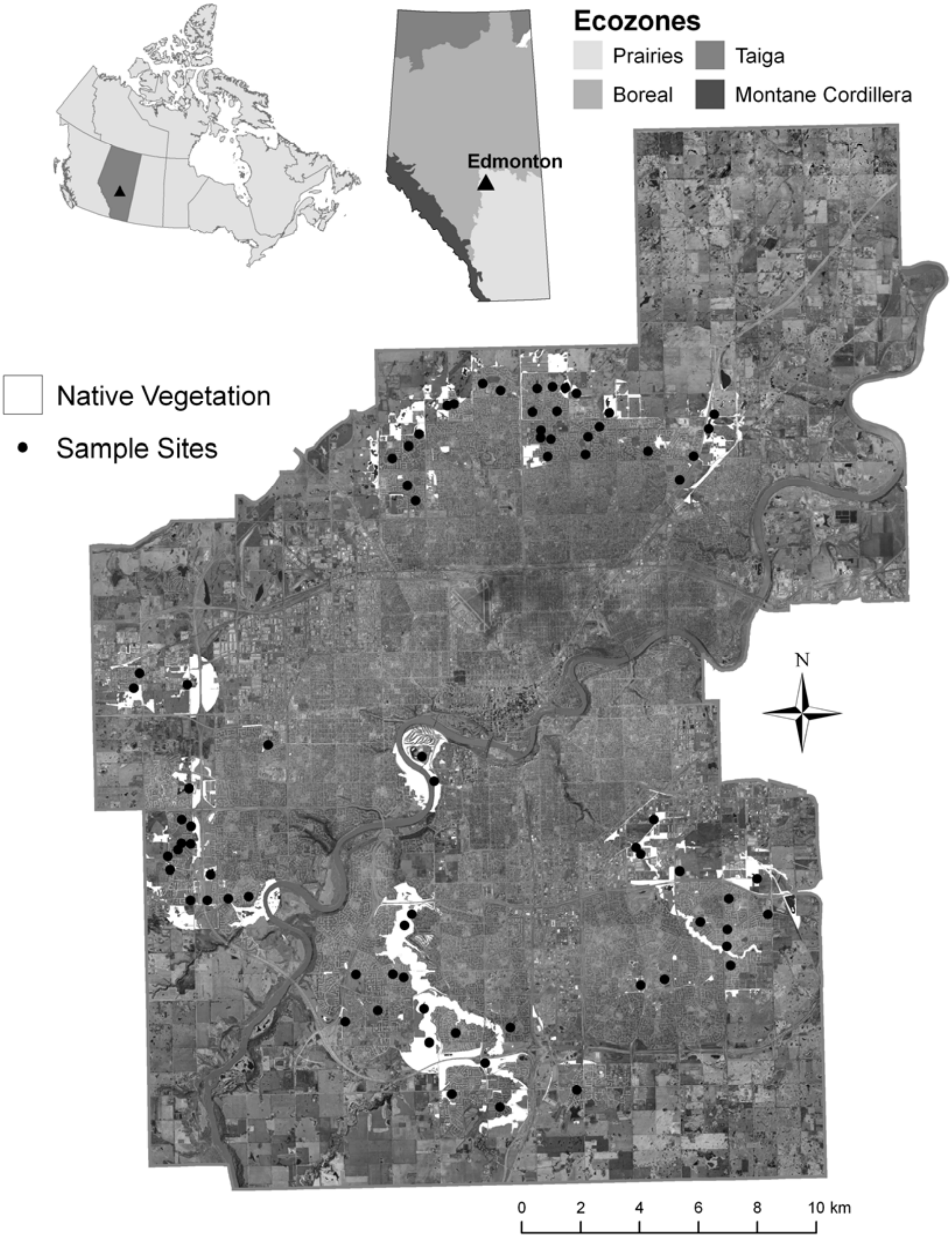

Fig. 3.1 Wetland locations in Edmonton, Alberta, Canada. The study area was located at the northern edge of the Aspen Parkland. White areas indicate native vegetation within 1000 m of wetlands.

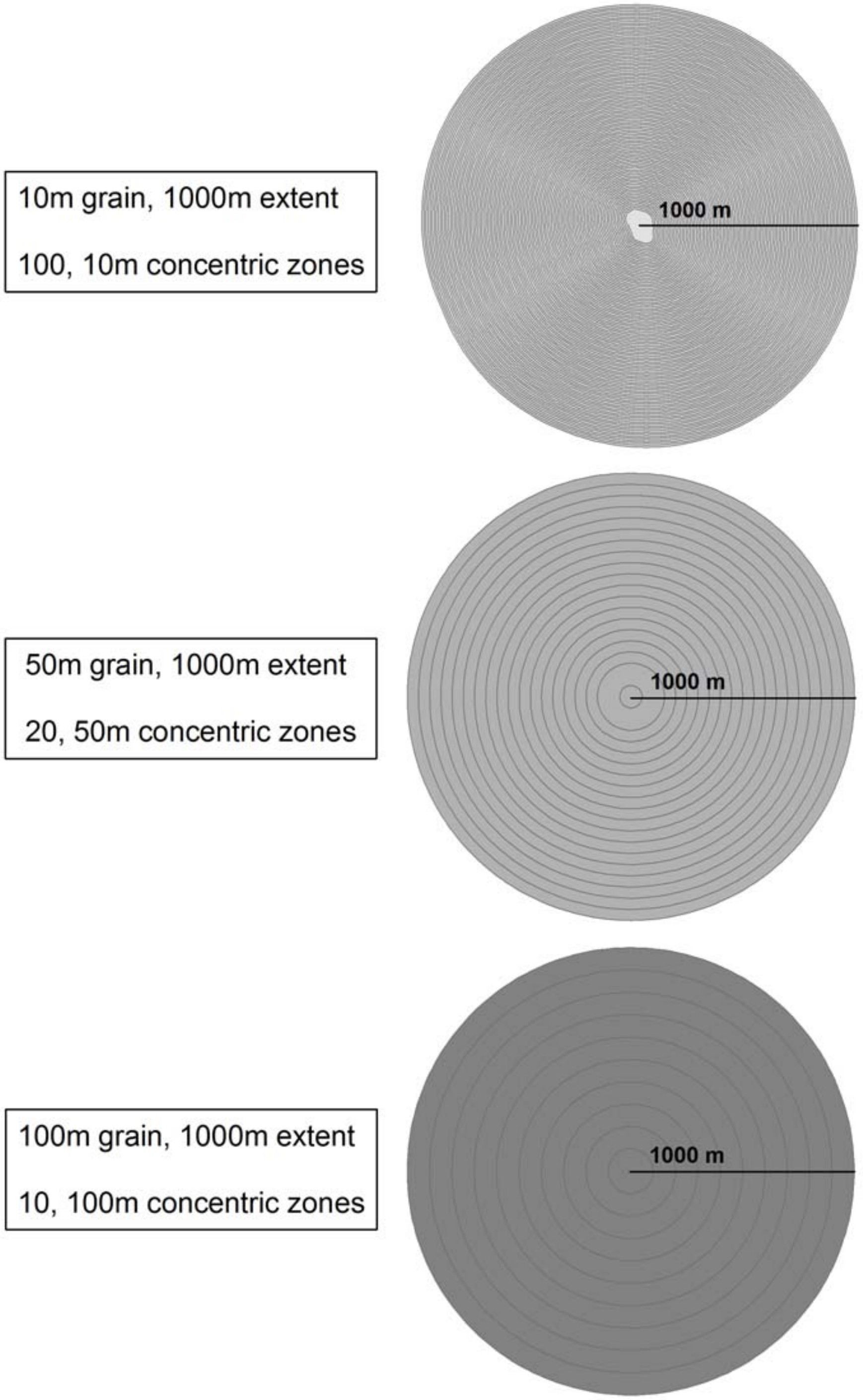

Fig 3.2 A visual representation of concentric zones of terrestrial habitat used in logistic regression. Center of each zone represents a single wetland.

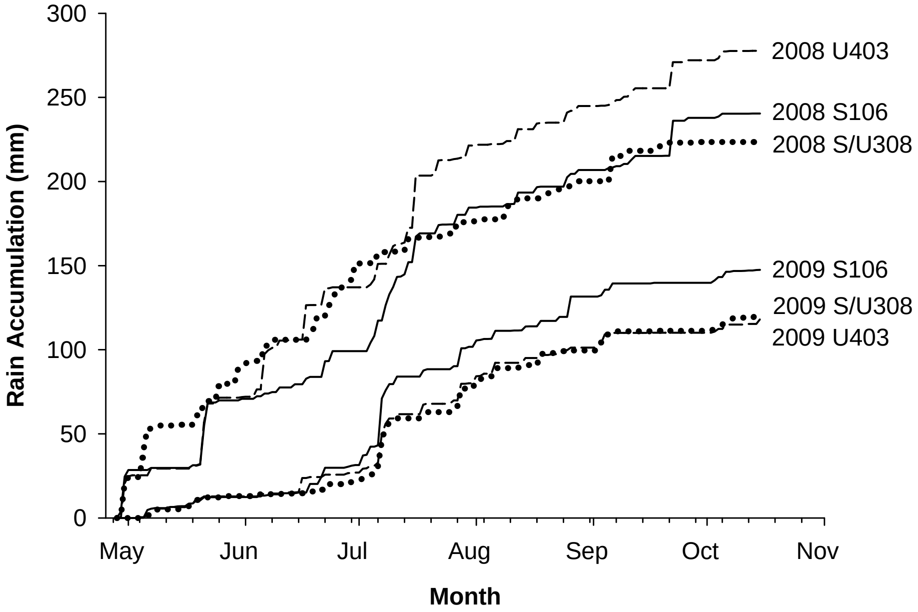

Fig. 3.3 A visual representation for the accumulation of rain taken from three different wetland locations in 2008 and 2009. All rain was collected by the City of Edmonton. More rain fell in 2008 than 2009 for all locations. Differences in rain from 2008 to 2009 ranged from 93 mm at site S106 to 160 mm at site U403. U403, S106, and S/U308 represent an upland wetland, stormwater wetland, and upland wetland integrated in stormwater management, respectively.

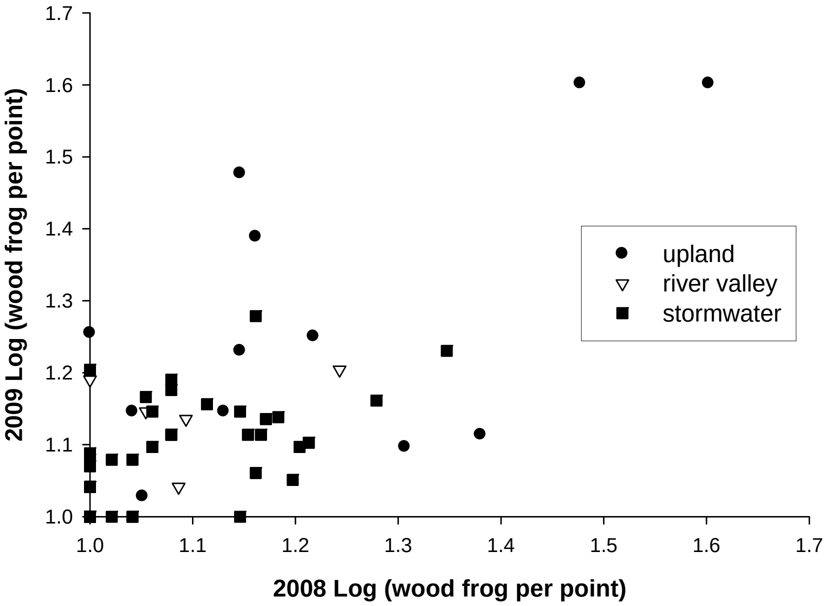

Fig. 3.4 Average number of calling wood frogs per Breeding Call Survey point for 2008 compared to 2009 in 74 of 75 study wetlands. In 2009, one stormwater wetland from the 75 surveyed in 2008 was destroyed. Spearman rank correlation between values for 2008 and 2009 reveals a significant correlation in number of calling males between years for stormwater wetlands only (upland, $r_s = 0.355$, $P < 0.257$; river valley $r_s = 0.100$, $P < 0.873$; stormwater, $r_s = 0.699$, $P < 0.001$).

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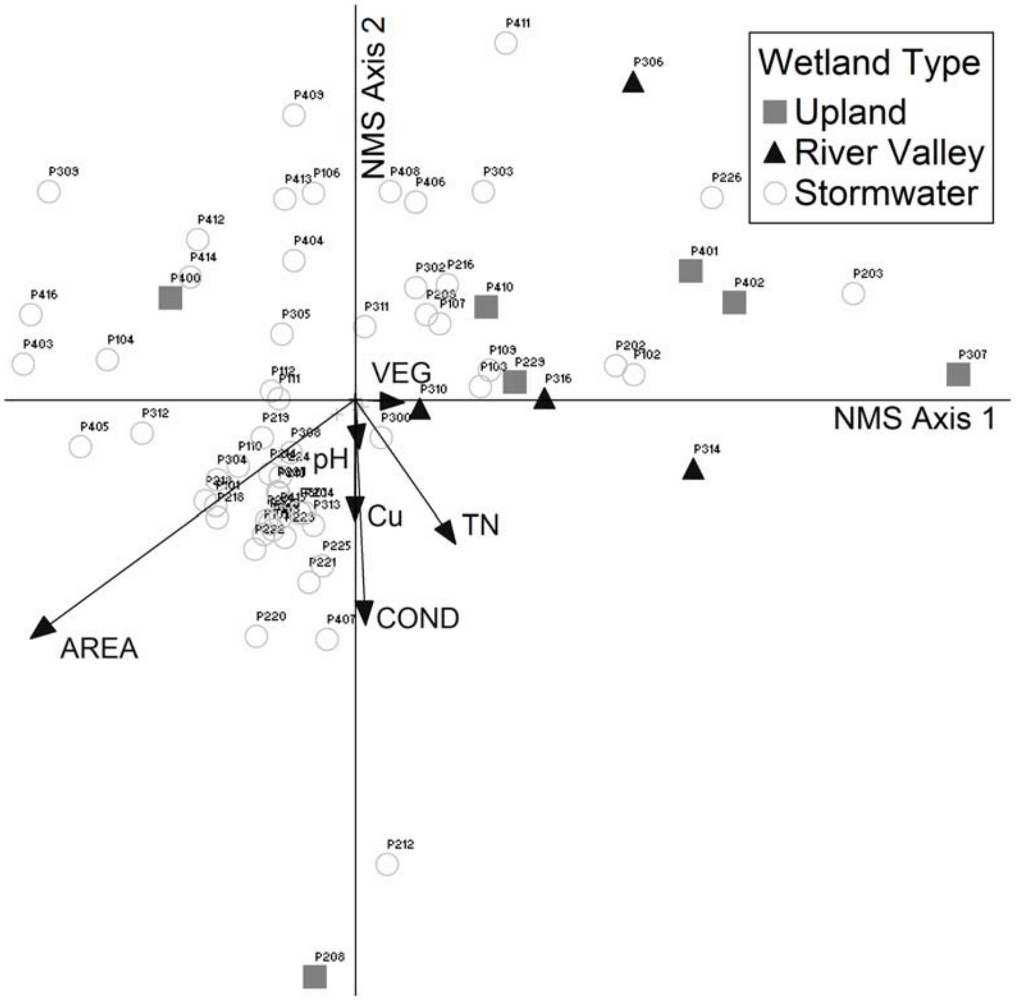

Fig. 3.5 Non-metric multidimensional scaling ordination plot of sample scores from 72 wetlands and 11 environmental features grouped by wetland type. NMS Axis 1 and 2 were plotted as they explained the highest combined proportion of variance in environmental features (0.800 out of 0.912).Vectors reflect the correlation between environmental variables and ordination scores, e.g., wetland area is most strongly correlated with ordination scores for axis 1 and axis 2 ($r^2 > 0.500$). Conductivity (cond) ($r^2 > 0.400$) and total nitrogen (TN) ($r^2 > 0.300$) are also correlated with the ordination scores for axis 1 and axis 2. All other variables were weakly correlated with ordination scores ($0.100 < r^2 < 0.300$). Abbreviations are described in table 3.1.

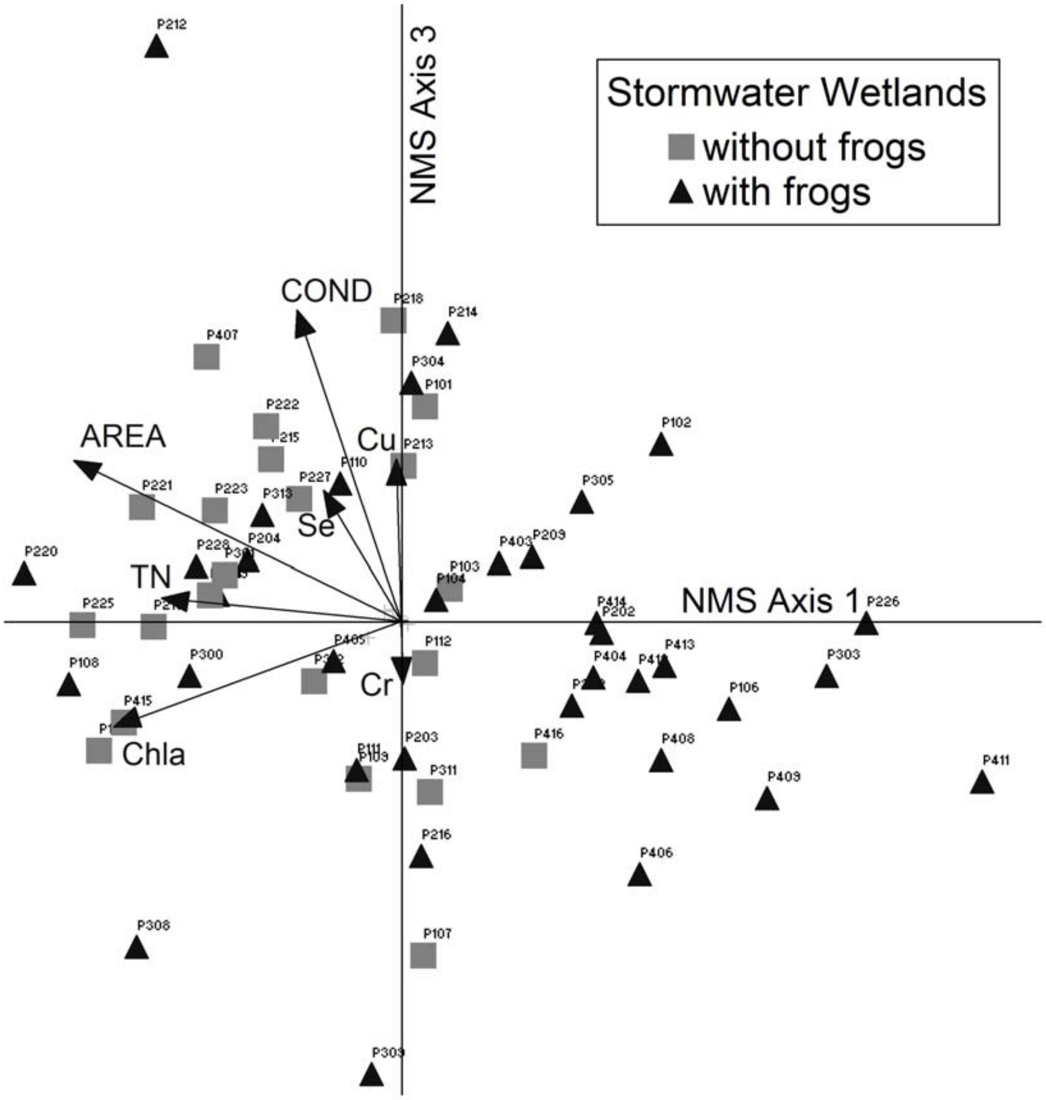

Fig. 3.6 Non-metric multidimensional scaling ordination plot of sample scores from 55 stormwater wetlands (with and without wood frogs) and 12 environmental features and year of construction. NMS Axis 1 and 3 were plotted as they explained the highest combined proportion of variance in environmental features (0.639 out of 0.899). Wetland area, chlorophyll-a (chla), conductivity (COND) were strongly correlated with ordination scores from axis 1 and axis 3 ($r^2 > 0.500$). Total nitrogen (TN) was moderately correlated ($r^2 > 0.400$). All other variables were weakly correlated with ordination scores ($0.100 < r^2 < 0.399$). Abbreviations are described in table 3.1.

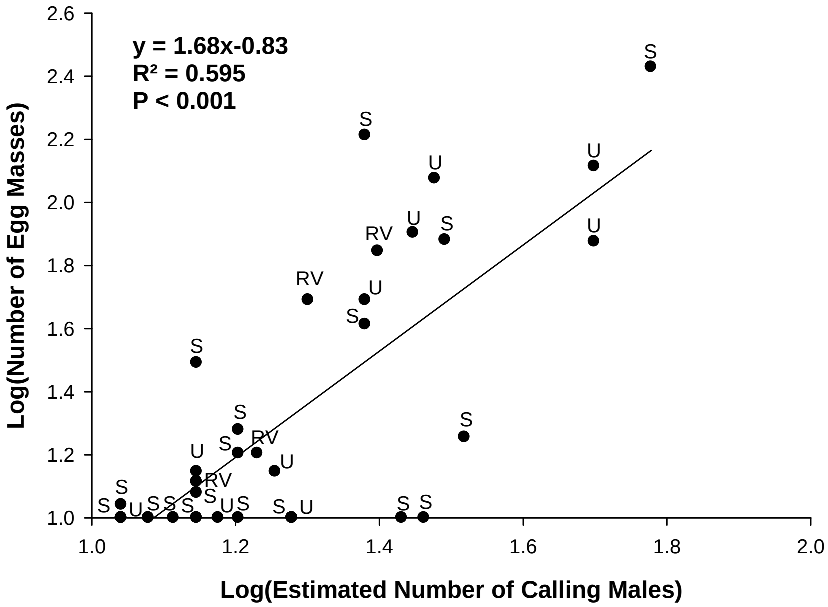

Fig. 3.7 The number of calling male frogs compared to egg masses at 42 urban wetlands in 2008. For each wetland (i.e., point on graph), egg mass counts were recorded the morning after call surveys for males. All points are labelled by wetland type stormwater (S), river valley (RV), and upland (U).

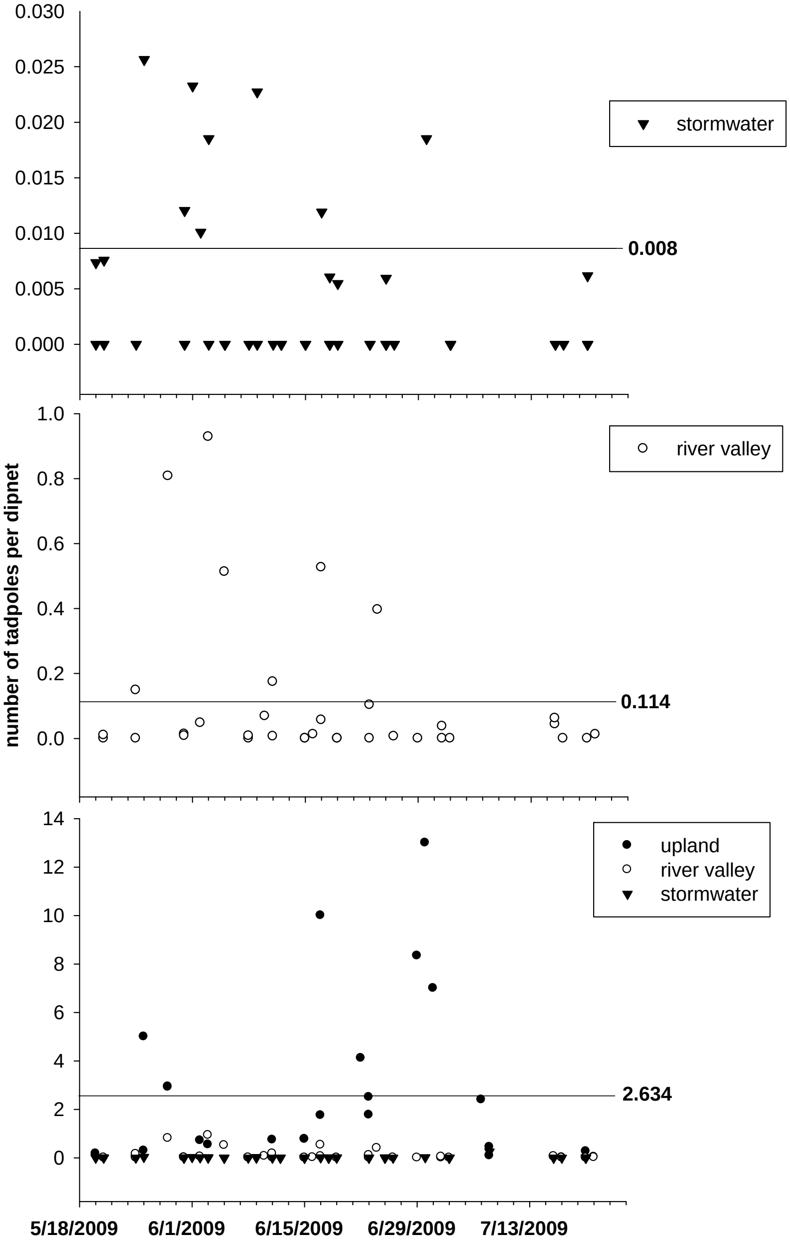

Fig. 3.8 The relative abundance of tadpoles for 13 focal wetlands from May to July, 2009 sampled with dip nets. Tadpole abundance was highest at upland wetlands and lowest at stormwater wetlands. Horizontal lines represent mean abundance across all surveys for each wetland type. Please note the difference in scale on the y-axis. Relative abundance is displayed for all three wetland types combined on the bottom figure to serve as a visual comparison between abundances at the same scale. Each point represents a single survey.

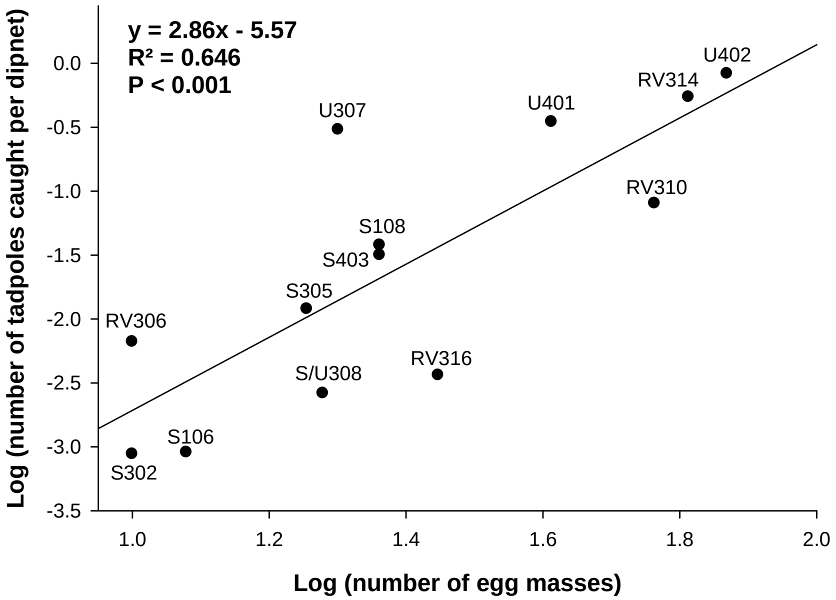

Fig. 3.9 A comparison between abundance of egg masses detected and relative abundance of tadpoles at 13 focal wetlands in 2009. The y-axis represents total number of tadpoles caught/total number of dipnet attempts. Each point is labeled by wetland type (stormwater (S), river valley (RV) and upland (U)) and unique identification number.

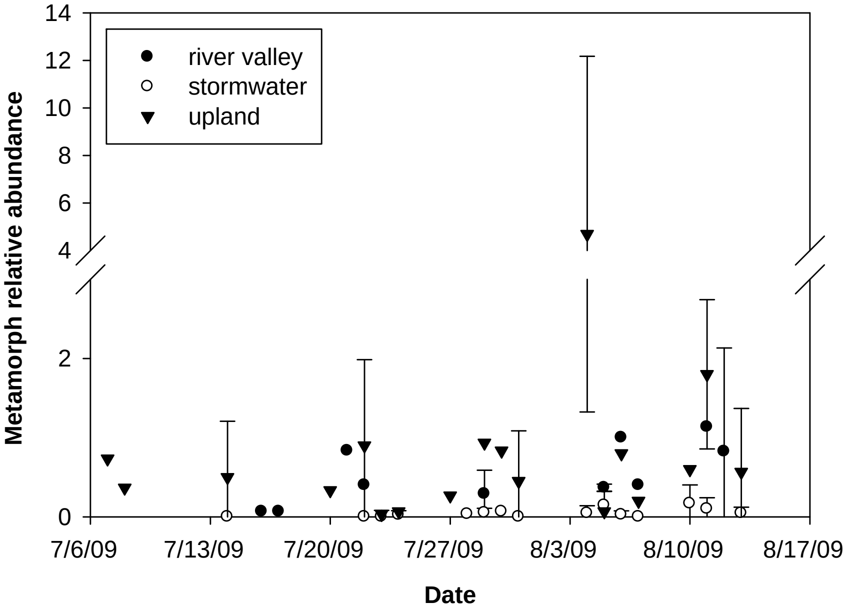

Fig 3.10 Metamorph relative abundance (total metamorphs caught/total survey time) was consistently higher at upland and river valley than stormwater wetlands in 2009. Each data point represents relative abundance averaged across wetland type for each survey date. The average number of wetlands surveyed per point was 1.5, 4, and 1.4 for river valley, stormwater, and upland wetlands, respectively. Bars represent standard deviation.

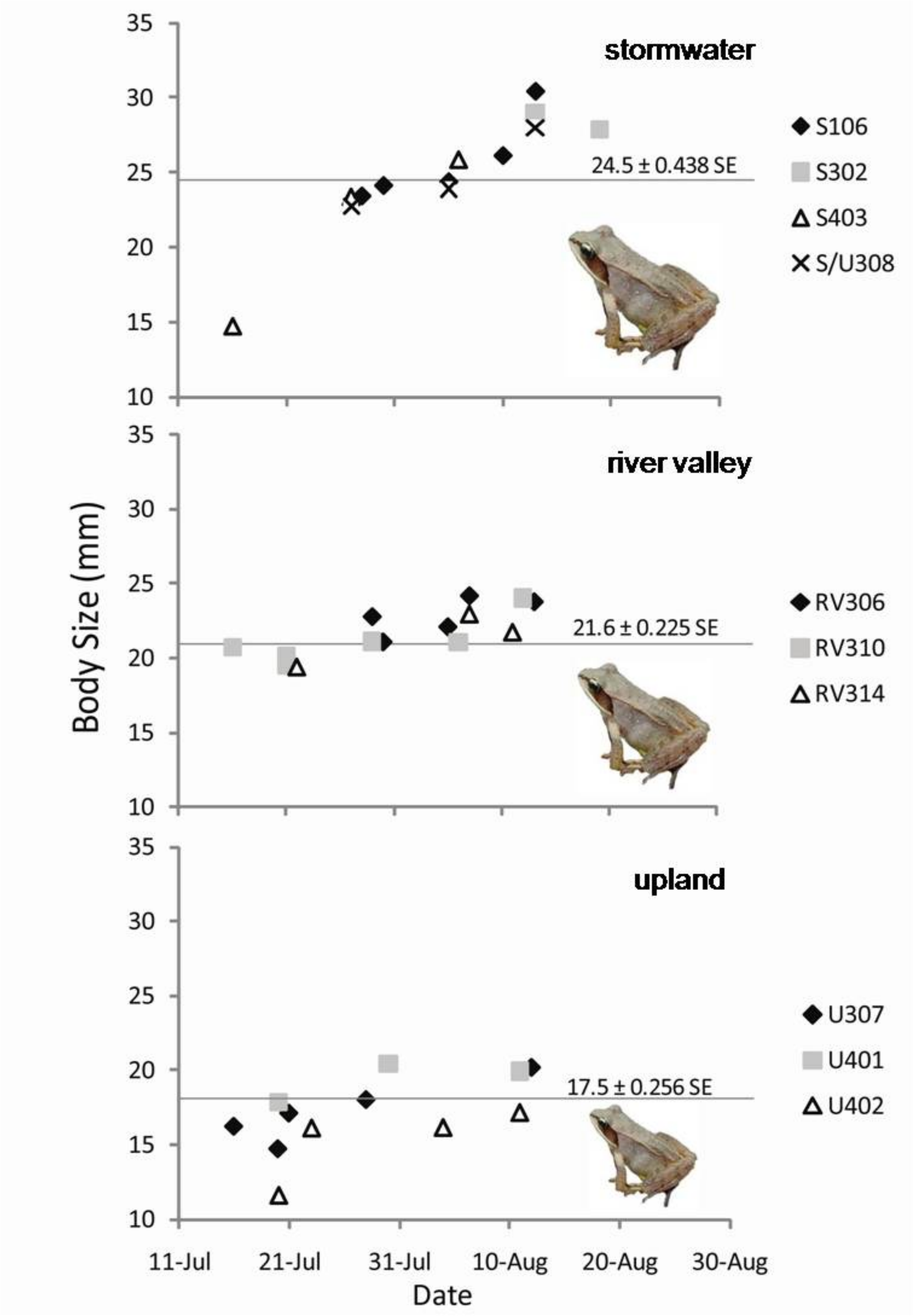

Fig. 3.11 Metamorph size for four stormwater, three river valley, and three upland wetlands from July 16 – August 19, 2009. All wetlands are part of the set of 13 focal sites. Horizontal lines represent mean metamorph body size (± standard error) for all populations across all sampling dates. Each point in the legend is labeled by wetland type (stormwater (S), river valley (RV) and upland (U)) and unique identification number. Each point on the graphs represents between 1 and 10 individuals. Images of frogs are scaled to represent the mean size of metamorphs in each of the three wetland types.

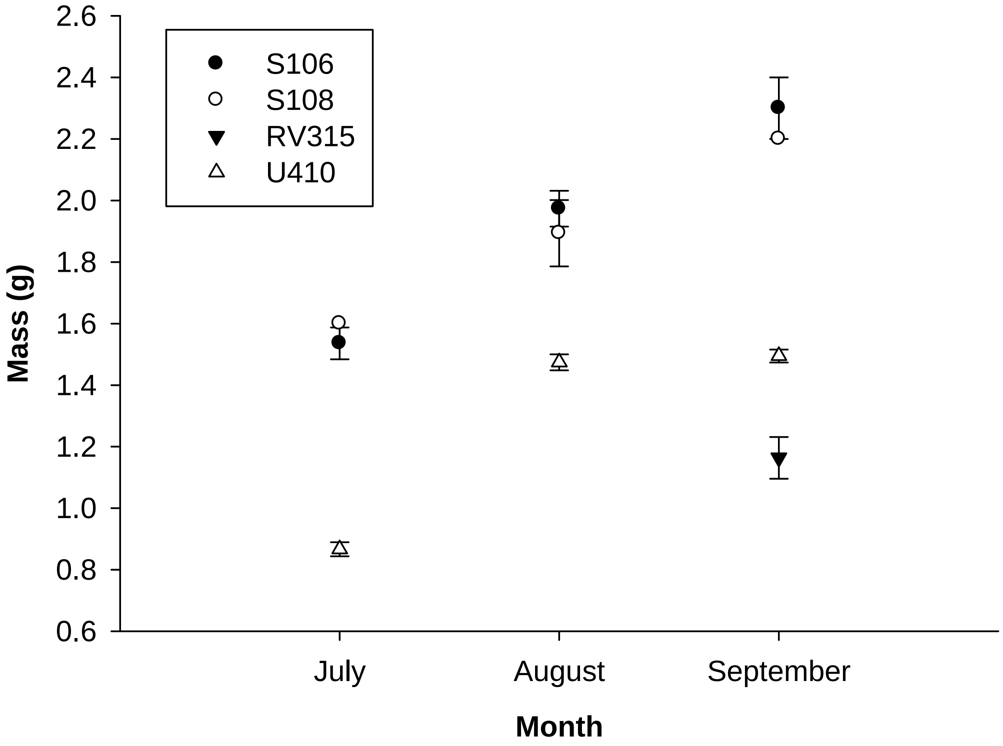

Fig. 3.12 Average mass of metamorphs/young-of-the-year caught at drift fences at two stormwater (S), one river valley (RV) and one upland (U) wetland in 2008. Bars represent standard error of mean. Points represent between 1 and 212 individuals. S108 was the only wetland with a sole individual. Most metamorphs migrated at S108 during August; thus, only one individual was recorded at S108 during July and one during September. These individual data points were not included in the statistical analysis but are included in this figure to illustrate the size of individuals found at this stormwater wetland.

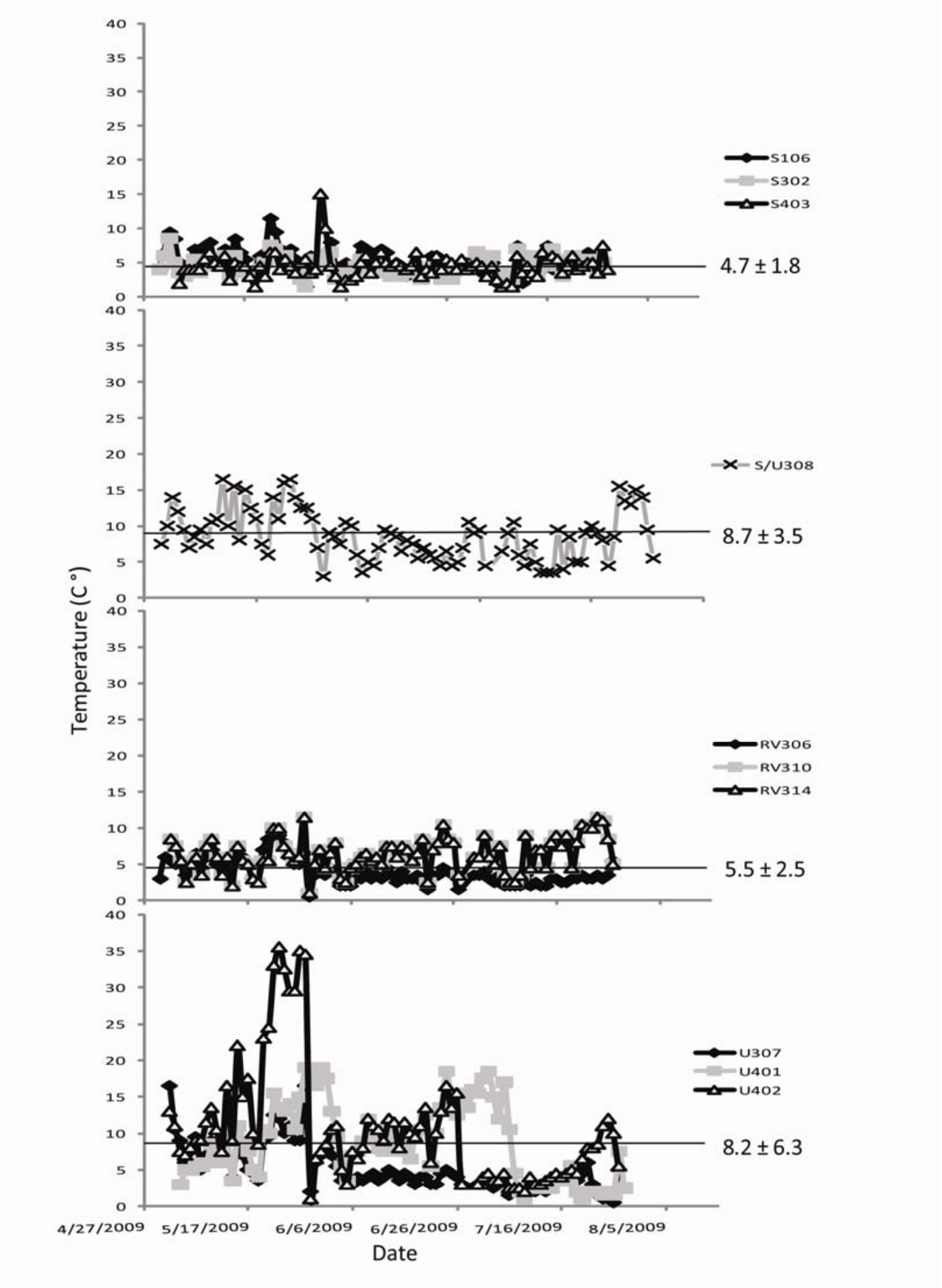

Fig. 3.13 Daily water temperature difference (maximum minus minimum) for four stormwater (S), three river valley (RV), and three upland wetlands (U) in 2009. Horizontal lines represent the average temperature difference (± standard deviation) for each wetland type.

Table 3.1. Summary of mean values and standard deviation (SD) for 16 environmental features recorded at upland, rivervalley, and stormwater wetlands in 2008. One-way ANOVA and non-parametric Kruskal-Wallis (KW) one-factor ANOVA are used to compare parameters between wetland types. Significant p-values (*alpha* ≤ 0.05) are in bold.

	Wetland Type					
Parameter	Upland (SD)	River valley (SD)	Stormwater (SD)	F/χ^2	*Df*	*P*
Year[a]	-	-	1997 (6)			
Area (m^2)[b]	16349 (28006)	3424 (2668)	16402 (12568)	5.832	2	**0.05**
H_2O Depth[b]	51 (26)	74 (22)	220	-	-	-
% VEG[bcs]	37 (19)	92 (6)	9 (17)	30.07	2	<**0.001**
SAV[des]	40 (35)	55 (14)	23 (24)	7.382	2	**0.02**
EMERG[fgs]	2 (2)	1 (1)	2 (1)	1.877	2	0.391
TN (µg/L)[hi]	5150 (5282)	1130 (376)	966 (514)	27.75	68	<**0.001**
TP (µg/L)[hj]	1506 (1659)	181 (177)	101 (100)	26.27	68	<**0.001**
Cond (µS/cm)[hk]	1514 (1464)	856 (421)	757 (421)	1.016	68	0.367
pH[h]	8.26 (0.4)	8.72 (0.6)	8.29 (0.7)	0.869	68	0.424
Chl-a (µg/L)[hl]	48 (46)	14 (20)	21 (24)	1.497	68	0.231
As (µg/L)[hms]	5 (4)	5 (3)	2 (1)	9.219	2	**0.009**
Cr (µg/L)[hns]	0.7 (1.3)	0.1 (0.1)	0.4 (0.4)	0.924	2	0.630
Cu (µg/L)[ho]	3 (3.9)	1.9 (0.9)	1.7 (1.4)	0.301	68	0.741
Pb (µg/L)[hp]	0.3 (0.2)	0.2 (0.1)	0.1 (0.1)	3.518	68	**0.035**
Se (µg/L)[hqs]	2.8 (3.8)	0.2 (0.2)	0.5 (0.4)	4.349	2	0.114
Zn (µg/L)[hr]	21 (19)	12 (13)	15 (13)	0.631	68	0.535

[a] N = 56

[b] N = 12, 5, 58

[c] percent native vegetation within 100 m

[d] submersed aquatic vegetation

[e] N = 6, 4, 56

[f] rank for emergent vegetation

[g] N = 11, 5, 58

[h] N = 10, 4, 57

[i] total nitrogen

[j] total phosphorus

[k] conductivity

[l] chlorophyll-a suspended in water

[m] arsenic

[n] chromium

[o] copper

[p] lead

[q] selenium

[r] zinc

[s] non-parametric KW test

Table 3.2. Summary of mean values and standard deviation (SD) for 16 environmental features recorded at a subset of 13 upland, river valley, and stormwater wetlands from 2008.

	Wetland Type		
Parameters	Upland (SD)	River valley (SD)	Stormwater (SD)
N	3	4	5
Year	-	-	2002 (2)
Area (m^2)	894 (182)	4008 (1548)	14375 (4495)
H_2O Depth	62 (9)	81 (22)	220
% VEG[a]	18 (6)	92 (4)	20 (10)
SAV[b]	38 (18)	55 (8)	24 (8)
EMERG[c]	1 (1)	2 (1)	3 (1)
TN (µg/L)[d]	2250 (985)	1130 (217)	1060 (296)
TP (µg/L)[e]	404 (97)	181 (102)	184 (69)
Cond (µS/cm)[f]	514 (514)	916 (577)	505 (225)
pH	8.5 (0.7)	8.5 (0.5)	8 (0.2)
Chl-a (µg/L)[g]	42 (30)	14 (11)	41 (19)
Chl-a (µg/L)[hi]	1.1070	0.846 (.194)	0.356 (.138)
As (µg/L)[j]	0.24 (0.09)	0.15 (0.09)	0.37 (0.56)
Cr (µg/L)[k]	3.47 (3.49)	2.97 (0.23)	2.08 (0.74)
Cu (µg/L)[l]	0.427 (.120)	1.903 (.501)	0.678 (.210)
Pb (µg/L)[m]	0.30 (.07)	0.16 (.04)	0.11 (.02)
Se (µg/L)[n]	0.43 (0.38)	0.2 (0.17)	0.26 (0.19)
Zn (µg/L)[o]	26.6 (8.7)	11.5 (7.5)	27.9 (10.3)

[a] percent native vegetation within 100m
[b] submersed aquatic vegetation
[c] rank for emergent vegetation
[d] total nitrogen
[e] total phosphorus
[f] conductivity
[g] chlorophyll-a suspended in water
[h] N=1,2,4
[i] substrate chlorophyll-a taken in 2009
[j] arsenic
[k] chromium
[l] copper
[m] lead
[n] selenium
[o] zinc

Table 3.3. Summary of mean values and standard deviation (SD) for 16 environmental features recorded at stormwater wetlands with (N = 35) and without (N = 21) wood frogs. One-way ANOVA and non-parametric Kruskal-Wallis (KW) one-factor ANOVA are used to compare parameters between stormwater wetlands with and without wood frog. Significant p-values (*alpha* ≤ 0.05) are in bold.

	Stormwater Wetlands				
Parameter	Present (SD)	Absent (SD)	F/χ^2	*df*	*P*
Year	1999 (4)	1992 (9)	10.61	55	**0.001**
Area (m^2)	14181 (14684)	19275 (8112)	6.936	55	**0.01**
H_2O Depth	220	220	-	-	-
% VEG[an]	35 (37)	23 (38)	3.596	1	0.06
SAV[bn]	26 (23)	20 (25)	1.605	1	0.205
EMERG[cn]	3 (1)	2 (1)	4.699	1	**0.03**
TN (µg/L)[d]	883 (574)	1096 (398)	2.139	55	0.149
TP (µg/L)[e]	98 (108)	111 (94)	1.553	55	0.218
Cond (µS/cm)[f]	719 (448)	841 (393)	1.657	55	0.203
pH	8.2 (0.7)	8.4 (0.7)	0.834	55	0.366
Chl-a (µg/L)[g]	18 (26)	27 (21)	4.066	55	**0.05**
As (µg/L)[h]	2 (1.3)	1.9 (1.1)	0.049	55	0.825
Cr (µg/L)[in]	0.3 (0.4)	0.5 (0.5)	4.803	1	**0.03**
Cu (µg/L)[j]	1.4 (1.5)	1.8 (1.1)	2.664	55	0.108
Pb (µg/L)[k]	0.1 (0.1)	0.2 (0.2)	1.793	55	0.186
Se (µg/L)[l]	0.3 (0.3)	0.7 (0.4)	11.23	55	**0.001**
Zn (µg/L)[m]	15 (15)	14 (10)	0.023	55	0.878

[a] percent native vegetation within 100 m
[b] submersed aquatic vegetation
[c] rank for emergent vegetation
[d] total nitrogen
[e] total phosphorus
[f] conductivity
[g] chlorophyll-a suspended in water
[h] arsenic
[i] chromium
[j] copper
[k] lead
[l] selenium
[m] zinc
[n] non-parametric KW test

Table 3.4. Occurrence and abundance for boreal chorus frog and tiger salamander at 75 wetlands surveyed in 2008 and 2009. (SD) denotes ± standard deviations. Wetland type is classified as U (upland), RV (river valley), and S (stormwater).

Species	Year - Metric	Type	N	Occ.[2]	% Occ.[3]	Abundance[4]	Abundance[5]
Boreal chorus frog	2008 BCS [1]	U	12	11	92	7 (5)	8 (5)
		RV	5	3	60	2 (3)	3 (4)
		S	58	26	45	2 (5)	4 (7)
	2009 BCS[1]	U	12	10	83	6 (9)	7 (9)
		RV	5	2	40	0.2 (0.3)	1 (0.1)
		S	57	10	18	1 (2)	4 (5)
Tiger salamander	2008 and 2009	U	12	3	25	N/A	N/A
		RV	5	3	60	N/A	N/A
		S	58	6	10	N/A	N/A

[1] Abundances for Breeding Call Surveys (2008 and 2009) for boreal chorus frog represent calling male frogs per survey point

[2] Occurrence

[3] Percent occurrence across wetlands sampled

[4] Abundance for all wetlands surveyed (both with and without amphibians occurrence)

[5] Abundance after removing all wetlands without amphibian occurrence

Table 3.5. The occurrence (A) and co-occurrence (B) of male wood frog (WF) and boreal chorus frog (BCF) at upland, river valley, and stormwater wetlands in 2008 and 2009.

A

		WF only	BCF only	Both	Neither	Total
2008	Upland	1	1	10	0	12
	River valley	1	0	3	1	5
	Stormwater	13	12	14	19	58
	Total	15	13	27	20	75
2009	Upland	2	0	10	0	12
	River valley	3	0	2	0	5
	Stormwater	22	1	9	25	57
	Total	27	1	21	25	74

B

	spp.	Absent	With other spp.	Alone
2008	BCF	35	27	13
	WF	33	27	15
2009	BCF	52	21	1
	WF	33	21	27

Table 3.6. Descriptive statistics for all life-history stages of the wood frog surveyed in 2008 and 2009. (SD) denotes ± standard deviations. Wetland type is classified as U (upland), RV (river valley), and S (stormwater).

Year - Metric	Type	N	Occ.[1]	% Occ.[2]	Abundance[3]	Abundance[4]
2008 BCS [5]	U	12	11	92	8 (9)	9 (9)
	RV	5	4	80	3 (3)	3 (3)
	S	58	27	47	2 (3)	4 (3)
2009 BCS[5]	U	12	12	100	11 (10)	11 (11)
	RV	5	5	100	4 (2)	4 (2)
	S	57	31	54	2 (2)	4 (2)
2008 EGG MASS[6]	U	11	9	75	54 (55)	62 (55)
	RV	4	4	100	27 (27)	27 (27)
	S	28	10	37	16 (51)	42 (79)
2008 TADPOLE[7]	U	10	9	90	11.9 (13.1)	13.2 (13.1)
	RV	4	4	100	1.3 (1.7)	1.3 (1.7)
	S	25	12	48	0.6 (1.4)	1.2 (1.8)
2009 METAMORPH[8]	U	11	9	82	1.5 (1.90)	1.8 (1.9)
	RV	4	4	100	0.42 (.28)	0.42 (0.28)
	S	30	9	30	0.03 (0.06)	0.11 (0.06)
2008 METAMORPH	U	12	9	75	N/A	N/A
	RV	5	5	100	N/A	N/A
	S	58	5	9	N/A	N/A

[1] Occurrence

[2] Percent occurrence of total

[3] Abundance for all wetlands surveyed (both with and without amphibian occurrence)

[4] Abundance after removing all wetlands without amphibian occurrence

[5] Abundances for BCS (2008 and 2009) are calling male frogs per survey point

[6] Abundances for egg mass (2008 and 2009) are counts

[7] Abundances for tadpoles are number of individuals caught per minnow trap

[8] Abundances for metamorphs are number of individuals caught per minute of sampling effort

Table 3.7. The percent land cover surrounding all 75 wetlands of each type and the percent of each land cover comprising the entire study area. All values represent the proportion of land cover within 100 m of each wetland type. All area within 100 m of each wetland type was pooled to give a single value that represents the proportion of each land cover type out of the total pooled area.

	Urban	Agriculture	Native Vegetation.	Wetland	River
Upland	36	17	37	10	0
River Valley	1	0	92	3	4
Stormwater	77	0	9	14	0
Total Landscape	65	3	19	12	1

Table 3.8. The terrestrial zones that best predict the occurrence of adult male wood frogs at 75 urban wetlands. A total of 130 regressions were performed in total. The top five models for each zone are reported. All zones with a ωi > .2 were considered substantial predictors of occurrence.

Zone	AICc Scale Comparison Rank	Model	AICc	ωi
10 m Zone	1	0-10 m	82.29	0.71
	2	990-1000 m	90.06	0.01
	3	250-260 m	90.13	0.01
	4	240-250 m	90.29	0.01
	5	260-270 m	90.41	0.01
50 m Zone	1	0-50 m	89.72	0.26
	2	950-1000 m	90.67	0.16
	3	200-250 m	91.20	0.13
	4	250-300 m	91.75	0.10
	5	850-900 m	92.27	0.07
100 m Zone	1	0-100 m	82.29	0.96
	2	100-200 m	92.26	0.01
	3	800-900 m	92.36	0.01
	4	700-800 m	92.71	0.01
	5	200-300 m	93.22	0.00

Table 3.9. Average relative abundance for multiple life-history stages surveyed at three different wetland types ("subset of wetlands") in 2009. (SD) denotes ± standard deviations. Wetland type is classified as U (upland), RV (river valley), and S (stormwater).

Type	N	Egg mass (counts)	Tadpole (# / dip net)	Metatmorph (# / min.)
U	3	35 (27)	0.49 (0.29)	1.40 (0.65)
RV	4	30 (26)	0.16 (0.26)	0.42 (0.33)
S	6	8 (5)	0.01 (0.02)	0.07 (0.07)

Table 3.10. Correlation coefficients for the relationship between water temperature and ambient air temperature for 10 wetland sites taken between May 1 – July 29, 2009. Max. represents the correlation coefficient between maximum water and air temperature. Min. represents minimum water and air temperature. Diff. represents the difference between maximum and minimum water and air temperatures. Large correlation coefficients represent strong linear relationships between water and ambient air temperatures. Significant p-values (by use of one-way ANOVA) represent significant differences in water and ambient air temperatures between wetland types.

	Wetland	Max	Min	Diff
CORRELATION COEFFICIENT	S106	0.857	0.912	0.583
	S302	0.784	0.922	0.569
	S403	0.812	0.900	0.569
	S/U308	0.845	0.904	0.572
	RV306	0.775	0.897	0.431
	RV310	0.837	0.897	0.582
	RV314	0.837	0.911	0.582
	U307	0.640	0.896	0.381
	U402	0.483	0.809	0.360
	U401	0.542	0.903	0.328
ANOVA	*F*	16.721	1.021	10.29
	df	3	3	3
	p	0.003	0.447	0.009

Note: all correlation coefficients were statistically significant at *alpha* = 0.002

Chapter 4

CONCLUSION

In the previous two chapters I identified gaps in research, as reported in recent literature, needed to provide conservation practitioners with the knowledge necessary to conserve urban amphibian population. I also provided evidence that stormwater wetlands can be used in urban landscapes to provide habitat for multiple life-stages of the wood frog.

As more and more of the world's human population moves to cities to live, habitat loss to urbanization is increasingly common (Butler and Laurance 2008). Urbanization represents a unique disturbance regime as many urban features (e.g., roads and parking lots) do not retain water and are completely impermeable. They therefore represent permanent habitat loss for wetland dependent species. These combined phenomena (impervious surface and permanent loss of habitat) undoubtedly threaten numerous species. Amphibians, for example, are especially susceptible to desiccation.

Conservation strategies based on local knowledge are imperative for maintaining local biodiversity in urban landscapes. My study was conducted in the northwestern part of the range for wood frog, boreal chorus frog and tiger salamander, all of which were found at stormwater wetlands. Other studies have shown the utility of human-made wetlands in supporting amphibian populations of various species (e.g., Barry et al. 2008), two of which explicitly examined the utility of urban wetlands as habitat for amphibians. For example, Brand and Snodgrass (2010) found six anuran species (*L. sylvaticus, Anaxyrus americanus, Pseudacris crucifer, Hyla chrysoscelis, Rana clamitans,* and *R. palustris*) present at artificial wetlands in Maryland, USA. Additionally, wetlands constructed on golf courses located in the urban setting of Stockholm, Sweden, contained four of five amphibian species that occurred in the study area (present: *Bufo*

bufo, Rana arvalis, Triturus vulgaris, and *T. cristatus*) (Colding et al. 2009). Stormwater wetlands likely play an important role in supporting amphibian species in urban landscapes, and in some cases (i.e., Brand and Snodgrass 2010 and Colding et al. 2009) have greater species richness and abundance than natural wetlands. Thus the general utility of stormwater wetlands as habitat for amphibians seems relatively widespread.

In Chapter 2, I proposed that more research examine the entire life cycle of amphibians. Conservation strategies based on data from a single life stage may be inherently inaccurate because organisms at different life stages have unique habitat requirements and respond differently to disturbances (Rothermel and Semlitsch 2002). Although (in Chapter 3) I conclude that stormwater wetlands do allow for successful reproductive recruitment (denoted by the presence of calling adult males, egg masses, larvae, newly metamorphosed young-of-the-year, as well as metamorphs emigrating away from stormwater sites), abundance and density of larvae and metamorphs were significantly lower at stormwater versus natural wetlands. Future research should investigate why abundances were lower at stormwater wetlands and how populations of amphibians at stormwater wetlands change over time in order improve the conservation potential of these sites.

A continuous forest zone of > 100 m around breeding wetlands may adequately maintain some amphibian assemblages over time (Burbrink et al. 1998); however, large terrestrial buffers are impractical in urban landscapes, particularly in *a posteriori* management. I recommend smaller scale evaluation of habitat features for amphibians in urban environments. For example, I found that wood frog presence at a wetland was best predicted by native vegetation at local scales between 0 – 100 m, scales that have been commonly overlooked in previous studies of urban amphibians. Wood frog populations would likely benefit from increased preservation of terrestrial habitat immediately surrounding stormwater wetlands, particularly within 10 m of wetland edge. Many wetlands in my study area already have a narrow zone of native vegetation (between 5 – 25 m in width), beyond which were large areas of mowed, manicured lawn. Because it is impractical to advocate large scale conservation "*a posteriori*" in highly developed environments, I suggest, at the very least, that these "mowed" areas be left fallow or restored to native vegetation. This approach will not only reduce long-term maintenance costs and further filter water run-off prior to entering the wetland, but will promote local biodiversity including long-term maintenance of amphibian populations (Semlitsch 1998). Public opinion in Edmonton, however, has been both for and against constructing non-manicured, naturalized stormwater wetlands. Therefore, for such a management plan to work, innovative education initiatives through land stewardship and citizen science programs may significantly help sway public opinion to restore natural vegetation surrounding these wetland habitats (as suggested in Calhoun et al. 2003 and Calhoun and Reilly 2008).

Lastly, I recommend that behavioral responses to urban habitat (e.g., constructed stormwater wetlands or altered urban terrestrial habitats) be studied in amphibians. By focusing on species' behavior, we can make educated management decisions that maximize the greatest utility of conservation dollars. In other words, we need to focus on areas that provide the "biggest bang for the buck". For example, substrate characteristics influence habitat selection and movements in salamanders and frogs (Smith et al. 2003; Rittenhouse et al. 2004). Thus, landscape scale movements between sub-populations cannot occur if the area immediately surrounding a breeding pond, with its array of microhabitats and local habitats, impedes an individual's ability to move. Metamorphosed amphibians orient non-randomly when emigrating from breeding ponds (Vasconcelos and Calhoun 2004). Therefore, maintaining habitat directly adjacent to breeding ponds is likely to be critical for the persistence of urban amphibian populations (Regosin et al. 2005; Trenham and Cook 2008; Walston and Mullin 2008). Such protection should be a bare minimum as populations would benefit by having even larger tracts of peripheral terrestrial habitat (Windmiller et al. 2008). Conservation would benefit from ecological and behavioral studies (e.g., those that identify cues associated with amphibian orientation in urban landscapes), particularly studies that identify local habitat features essential in maintaining amphibian populations in urban landscapes.

Information on movement capabilities of amphibians are currently lacking in urban literature. In addition to Paton et al. (2008), I am aware of only one other study (see Husté et al. 2006) that uses radio telemetry to examine movement patterns of individual amphibians in an urban landscape. In addition, Birchfield and Deters (2005) is the only study to date to have used alternative tracking methods such as fluorescent powder to monitor amphibian movements or examine habitat selection in urban landscapes (see Rittenhouse et al. 2004 and Graeter et al. 2008 for details on powder tracking amphibians).

Husté et al. (2006) used radio telemetry to examine Natterjack Toad (*Bufo calamita*) movements in an urban park near Paris, France, and discovered the species had high site-fidelity and reduced dispersal and reduced homing ability compared to other, non-urban populations. In addition, they found that toads hid during the day under rocks arranged around artificial wetlands, in burrows of small rodents, and under stairs of a playground. These data highlight key features of urban designs that promote Natterjack toad persistence. Husté et al. (2006) identified high winter mortality and decreased dispersal abilities in their study population, and suggested that future management should increase over-wintering sites such as mounds of stacked rocks immediately adjacent to breeding ponds. Findings from studies similar to Husté et al. (2006) are absent from the North American literature, yet can assist land managers in improving habitat quality to sustain local, urban amphibian populations.

Understanding how density affects individuals at different life-stages in man-made and natural systems may also provide useful information for management. For example, if I were to manage urban systems strictly based on adult occurrence at my study wetlands, I would conclude that maintaining natural wetlands and terrestrial habitat is most important for conserving wood frog populations in my study area. However, my research also demonstrated that stormwater wetlands support larvae and metamorphs, and that frogs reared in stormwater wetlands were significantly larger than those from natural wetlands. Larger size of newly recruited individuals from stormwater wetlands may have both survival and reproductive advantages. Despite these growth advantages, post-metamorphic mortality in urban environments is likely high considering the lack of terrestrial habitat surrounding stormwater wetlands, which in turn may explain why adult populations remain low.

As a prerequisite for urban development, stormwater wetlands must be created to prevent flooding and to aid water purification. Considering the creation of breeding habitats via stormwater wetlands, urban wood frog populations may be better served by preservation of terrestrial habitat surrounding stormwater wetlands rather than purchasing natural wetlands. Allocating financial resources towards purchasing or restoring terrestrial habitat surrounding stormwater wetlands will not only provide habitat for pre-existing amphibian populations, but may also aid amphibian colonization of future stormwater sites.

LITERATURE CITED

Barry, D. S., T. K. Pauley, and J. C. Maerz. 2008. Amphibian use of man-made pools on clear-cuts in the Allegheny Mountains of West Virginia, USA. Applied Herpetology **5**:121-128.

Brand, A. B. and J. W. Snodgrass. In press. Value of artificial haibtats for amphibian reproduction in altered landscapes. Conservation Biology doi10.1111/j.1523-1739.2009.01301.x

Birchfield, G. L. and J. E. Deters. 2005. Movement paths of displaced Northern Green Frogs (Rana clamitans melanota). Southeastern Naturalist **4**:63-76.

Burbrink, F. T., C. A. Phillips, and E. J. Heske. 1998. A riparian zone in southern Illinois as a potential dispersal corridor for reptiles and amphibians. Biological Conservation **86**:107-115.

Butler, R.A., and W.F. Laurance. 2008. New strategies for conserving tropical forests. Trends in Ecology and Evolution **23**: 469-472.

Calhoun, A. J. K. and P. deMaynadier. (ed.) 2008. Science and conservation of vernal pools in Northeastern North America. Taylor and Francis Group. Boca Raton, FL, USA.

Calhoun, A. J. K. and P. Reilly. 2008. Conserving vernal pool habitat through community based conservation. p. 319-341. In Calhoun, A. J. K. and P. deMaynadier. (ed.) 2008. Science and conservation of vernal pools in Northeastern North America. Taylor and Francis Group. Boca Raton, FL, USA.

Colding, J., J. Lundberg, S. Lundberg, and E. Andersson. 2009. Golf courses and wetland fauna. Ecological Applications **19**:1481-1491.

Graeter, G. J., B. B. Rothermel, and J. W. Gibbons. 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. Journal of Wildlife Management **72**:473-482.

Husté, A., J. Clobert, and C. Miaud. 2006. The movements and breeding site fidelity of the natterjack toad (*Bufo calamita*) in an urban park near Paris (France) with management recommendations. Amphibia-Reptilia **27**:562-568.

Rittenhouse, T. A. G., M. C. Doyle, C. R. Mank, B. B. Rothermel, and R. D. Semlitsch. 2004. Substrate cues influence habitat selection by spotted salamanders. Journal of Wildlife Management **68**:1151-1158.

Rothermel, B. B. and R. D. Semlitsch. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology **16**:1324-1332.

Smith, G. R., A. Todd, J. E. Rettig, and F. Nelson. 2003. Microhabitat selection by Northern Cricket Frogs (*Acris crepitans*) along a west-central Missouri Creek: Field and Experimental Observations. Journal of Herpetology **37**:383-385.

Trenham, P. C. and D. G. Cook. 2008. Distributions of migrating adults related to the location of remnant grassland around an urban California tiger salamander (*Ambystoma californiense*) breeding pond. In: Mitchell, J.C., Jung Brown, R.E., Bartholomew, B., (Eds.), Urban Herpetology. Society for the Study of Amphibians and Reptiles, Salt Lake City, pp. 33-40.

Walston, L. J. and S. J. Mullin. 2008. Variation in amount of surrounding forest habitat influences the initial orientation of juvenile amphibians emigrating from breeding ponds. Canadian Journal of Zoology-Revue Canadienne De Zoologie **86**:141-146.

Windmiller, B. S., and A. J. K. Calhoun. 2008. Conserving vernal pool wildlife in urbanizing landscapes. In: Calhoun, A. J. K., deMaynadier. P.G., (Eds.), Science and conservation of vernal pools in Northeastern North America. CRC Press, Boca Rotan, pp. 233-251.