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The effects of urbanization on North American amphibian species: Identifying new directions for urban conservation

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Abstract Urbanization is a pervasive and growing threat to amphibian populations globally. Although the number of studies is increasing, many aspects of basic amphibian biology have not been investigated in urban settings. We reviewed 32 urban studies from North America and quantified the number of species studied and their response to urbanization. We examined existing research on breeding habitats, life-history stages, movement patterns, and habitat use relative to urbanization. We found amphibians as a whole respond negatively to urbanization (69 reported responses were negative, 6 were positive and 35 showed no effect). We caution, however, that many North American species still lack or are associated with conflicting information regarding species-specific responses (e.g., 89 potential responses were unknown). Approximately 40% of all anuran and 14% of caudate species in North America were investigated in the literature; however, the most diverse genera (e.g., *Plethodon* and *Eurycea*) were the most understudied likely due to their cryptic terrestrial lifestyles and biases in sampling protocols that assess wetland habitats via call surveys. Research on movement and small scale habitat use was deficient. Adult, juvenile, tadpole, and egg mass life-history stages commonly served as direct measures of species presence and abundance; however, such data do not accurately reflect recruitment into subsequent age classes and population persistence. The lack of data on many North American species may be contributing to poor management of urban amphibian populations and their habitats.

Keywords Habitat · Life-history · Management · Movement · Species diversity

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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 and 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. 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 and McDonnell 2008). More importantly, studies of urban amphibian ecology are relatively uncommon (Windmiller and Calhoun 2008; Mitchell et al. 2008) and recent literature (Hamer and 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, we review information on urban amphibian conservation that has not been addressed by previous reviews (e.g., Hamer and McDonnell 2008 and Mitchell et al. 2008). We quantify the number of amphibian species studied in urban settings, and characterize species specific responses to urbanization. We reviewed each paper and collated information on several variables we believe play an important role in urban conservation such as life-history stages considered in each study, breeding habitats of all studied species, sampling protocols used and other variables such as whether or not a study considered micro-habitat use or movement patterns.

Methods

Collating data from urban amphibian studies

We use the peer-reviewed literature to examine common themes that emerge from North American urban studies. We used two primary sources to find articles on urban amphibian ecology: Hamer and McDonnell (2008) and Mitchell et al. (2008). All studies were constrained to North America and published no earlier than 1990 and no later than 2008. We reviewed 20 primary scientific literature sources on urban amphibian ecology from Table 1 in Hamer and McDonnell (2008). From Mitchell et al. (2008) we reviewed six empirical studies from Sections "Introduction", "Methods", "Results" and "Discussion".

We 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 our review as they explicitly examined urban amphibian ecology. Three additional studies that were cited by studies reviewed in Hamer and McDonnell (2008) were included in our

Table 1 The number of species considered in 32 urban studies in North America

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

The heading A/C represents whether study considered Anura (A), Caudata (C) or both (A & C) review. In total, we reviewed 32 studies (Table 1): 20 from Hamer and McDonnell (2008), six from Mitchell et al. (2008), three from our ISI search, and three cited in literature reviewed by Hamer and McDonnell (2008).

Species-specific responses to urbanization

We 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) (similar to Fahrig and Rytwinski 2009). 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 (i.e., native habitat) over urban sites. We relied on the authors of each study to assess responses. For example, Rubbo and Kiesecker (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 environments 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, we 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, we 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, we evaluated species' responses based on figures and tables that distinctively indicated specific responses to urbanization. All species-specific responses were tallied and we summarized responses to urbanization across all amphibians studied.

What has been studied in urban amphibian ecology?

We 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.

Taxonomic groups studied and sampling methods

In order to determine which proportion of North American amphibians were studied in urban literature, we recorded all anuran and caudata species in North America recognized by Crother (2000) and all species studied within the 32 urban studies (Genus names following that of Crother 2000). The only exception was the *Ambystoma laterale-*

jeffersonianum complex where we 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). We 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). We 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, we 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), we 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.

Life-history stages

We 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.

Results

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. 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).

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. 1). 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. 1).

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). Our 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). 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

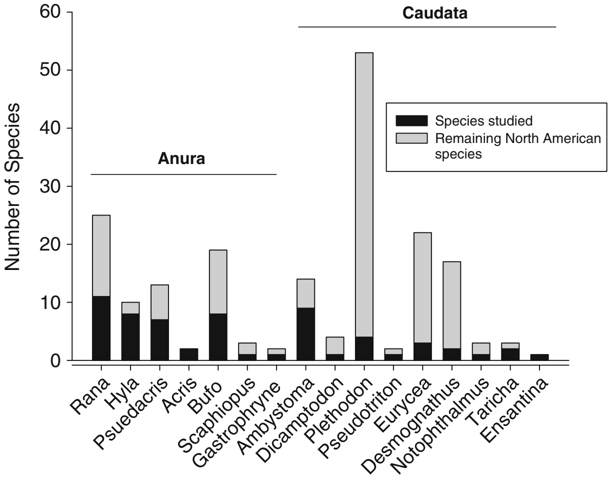

Fig. 1 The number of species (*N*=62) for each genus investigated in urban environments by 32 studies conducted between 1990 and 2008 compared to the number of North American species not studied for each genus (*N*=261)

majority of responses, i.e., 43% (83/193), however, were unknown (Table 2). Of the 32 North American amphibians threatened by urbanization according to IUCN 2010, only six were represented by studies in the urban literature (*Ambystoma californiense*, *Bufo boreas*, *Dicamptodon tenebrosus*, *Hyla femoralis*, *Rana capito*, *Rana aurora*) and only three responses (1 positive; *B. boreas*, 1 negative; *R. aurora*, and 1 neutral; *A. californiense*) were recorded. Amphibians that breed in wetlands and wetlands or streams have received the most attention in urban environments. Wetland or stream breeders is one of the least species-rich breeding guilds for caudates, but the most species-rich anuran guild (Table 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 13% 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 sub-adult life-history stages, 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 and Deters 2005).

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. One study compared

Table 2 The total number of species-specific responses (negative, positive, neutral, and unknown) collated by genus for 32 urban studies

Genus	Number of species	Total responses				Sources
		negative	positive	neutral	unknown	
Rana	11	18	2	12	35	1,4,5,6,7,8,9,10,11,12,13,14,15,16,17,21,22,23,25,27,28,21,32
Hyla	8	12	0	2	8	1,4,7,9,12,14,15,16,21,23,26,27
Psuedacris	6	7	1	6	12	1,4,7,9,10,11,14,15,16,20,21,22,23,25,27
Acris	2	2	0	0	3	1,4,7,15,23
Bufo	8	4	3	4	10	1,4,7,9,11,12,14,15,16,17,21,23,25,26,27
Scaphiopus	1	1	0	0	0	7
Gastrophryne	1	0	0	1	0	7
Eleutherodactylus	1	1	0	0	0	7
All Anura	38	45	6	25	68	
Ambystoma	9	7	0	6	9	1,6,8,10,12,13,14,16,20,22,25,27,28,29,31
Dicamptodon	1	0	0	0	1	25
Plethodon	4	3	0	2	1	1,10,14,19,25
Pseudotriton	1	1	0	0	0	1
Eurycea	3	6	0	0	0	1,3,18,24,30
Desmognathus	2	3	0	0	0	1,24,30
Notophthalmus	1	3	0	2		10,12,14,16,27
Taricha	2	1	0	0	3	20,22,25,26
Ensantina	1	0	0	0	1	25
All Caudata	24	24	0	10	15	
All Amphibian Species	62	69	6	35	83	

Source ID numbers are provided in Table 1

Table 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

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).

Discussion

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). 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).

Limitations in urban amphibian ecology

We 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, we 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. We provide three examples from our review to illustrate the limits of our knowledge:

a) According to our analysis, many North American species respond negatively to urbanization. Migration and dispersal are essential to the long-term persistence of most amphibian species found in North America (Semlitsch 2008). Thus, a species response to urbanization may be largely governed by it movement capabilities. Why certain amphibian species respond differently to fragmentation remains largely uncertain as few studies examine whether amphibians can effectively move through urban landscapes. Gibbs (1998) 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. If species with the capability of moving greater distances (or require long-distance migrations) 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? Only by studying amphibian movements in urban landscapes will we be able to effectively answer this question.
b) Of the 65 species investigated in our 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?" We 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.
c) In order to improve urban amphibian conservation 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 features (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. 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 and Semlitsch 2002). Urban sites resemble open-canopy natural vegetation (Birchfield and Deters 2005; Paton et al. 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 and Todd 2007). However, this explanation is speculative because microhabitat and movements in urban landscapes have rarely been examined globally (exceptions are Paton et al. 2008; Husté et al. 2006 and Birchfield and 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 et al. 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 and Deters 2005). Although these preferences may be a response to higher than average precipitation (Birchfield and 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.

One area of urban amphibian ecology that has received increasing attention is the utility of stormwater wetlands as habitat for amphibians. Some human-made habitats are inhabited by amphibians because they are analogues of natural habitats (Brand and Snodgrass 2010). These wetland types appear to be becoming widespread in urban areas, Kok et al. 2000; Kennedy and Mayer 2002). For example, pond-breeding amphibians likely regard artificial ponds as suitable breeding habitat as many ponds contain suitable within-wetland attributes (e.g. emergent vegetation) that likely promote successful reproduction comparable to natural sites (Brand and Snodgrass 2010). Reproduction at these sites may however be detrimental to the population if certain within-wetland paramters negatively affect reproductive recruitment (e.g. due to exotic predatory fish, pollution, altered hydrology that does not match the species' life history). Such sites may be regarded as ecological traps (Battin 2004). This is another area of urban amphibian ecology that warrants increased study as certain urban landscape features may become (e.g. retention ponds) or may contribute to (e.g. roads) ecological traps.

Amphibian groups considered in urban amphibian ecology

Our 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 our data, which shows that terrestrial breeding salamanders, though the most species-rich, are the most understudied North American amphibians in urban environments. It is important to note that it is possible that some taxa are understudied, e.g., terrestrial breeding salamanders, because these species are not generally present in highly urbanized landscapes. Though this may be true, future research that documents these species in areas pre- and post- urban development will provide useful information on understudied species vulnerable to urbanization.

One area of the North America that can benefit from increased research on urbanization is the Southeastern USA. 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 we strongly suggest future research focus on cities there.

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 and Fahrig 2007), larval sampling (Rubbo and Kiesecker 2005), visual and auditory surveys (Houlahan and 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. We 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 newly metamorphosed juveniles. 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 and Semlitsch 2002; Rothermel 2004; Lowe 2005). Hence, management of a species based on data from a single age class may be counter-productive (Rothermel and 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 and 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 young-of-year) as a response variable (as done in Windmiller et al. 2008).

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, we make the following recommendations for future studies that can help address on-the-ground conservation and management:

a) 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 (Baldwin and deMaynadier 2009).

b) Species-specific responses are essential to management: Our 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 and site-specific responses to urbanization to allow for effective population-level management (Cushman 2006).

c) 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 and Rothermel 2003).

d) 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. We advocate the future analysis of multiple response variables (including multiple life-history stages) to both aquatic and terrestrial habitat parameters.

e) 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. 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).

Conclusion

Our 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). Interfacing urban metrics with the complex life cycle of amphibians by including multiple life-history stages will likely yield valuable information regarding the negative impacts of urban development on amphibian populations. Furthermore, information regarding amphibian movements and habitat preferences should allow for spatially explicit land management plans that will protect urban amphibian populations through time.

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