University of Alberta

Postbreeding movement patterns and multiscale habitat use of adult wood frogs (*Lithobates sylvaticus*) at urban wetlands of Edmonton, Alberta.

by

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Abstract

Many studies have focused on the effects of urbanization on amphibian species richness, abundance and diversity, but few studies have quantified the effect on amphibian movement behaviour or habitat use. At 11 urban wetlands in Edmonton, Alberta, I examined the postbreeding movement behaviour and habitat use of adult wood frogs (*Lithobates sylvaticus*) from April through October using radio telemetry. I found that movement from breeding wetlands was limited, with most tracked individuals remaining within 25 m of ponds in grassy riparian zones. Long-distance migratory movements were rare and only occurred at sites with a high proportion of forested land-cover surrounding the wetland. Tracked frogs showed a preference at three spatial scales for habitat close to water that provided shelter from desiccation and predation (e.g. unmowed grass and stands of shrubs). These findings have implications for the management of wetlands and conservation of amphibian populations in urban settings.

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Chapter 1. General Introduction

Globally, the human population occupying urban areas has almost quadrupled since 1950 (UNHSA 2011). Despite the majority of urbanization occurring in the developing world, many cities throughout North America have also experienced massive increases to their populations over the past century (Hamer and McDonnell 2008; Mitchell and Brown 2008). As urbanization causes significant changes to the physical, chemical and ecological components of ecosystems, it is considered among the greatest threats to biota worldwide (Czech et al. 2000; Miller and Hobbs 2002).

Worldwide declines of amphibians have been well documented over the past several decades. Globally, amphibians have the highest proportion of species listed as threatened of any vertebrate class (Baillie et al. 2004; Stuart et al. 2004). Habitat loss, including that caused by urbanization, ranks among the most pervasive threats to amphibians with an estimated 88% of threatened amphibians under direct pressure from anthropogenic land-use change (Stuart et al. 2004; Cushman 2006). Most amphibians have a biphasic life history, relying on both aquatic habitat (for breeding and development of young) and terrestrial habitat for dispersal, migration, foraging and hibernating. As urbanization often involves the alteration and destruction of both aquatic and terrestrial land-cover, amphibians are especially vulnerable to such effects (Semlitsch 2002; McKinney 2006). Not only do anthropogenic land-use changes reduce available habitat for amphibians, they can also increase distances between remaining patches of suitable habitat, which can lead to population isolation, thus reducing the potential for recolonization should local extinctions occur (Semlitsch and Bodie 1998; Semlitsch 2000; Guerry and Hunter 2002). As many amphibians are important components of both wetland and terrestrial ecosystems, acting as both predator and prey species as well as accounting for a significant transfer of energy from aquatic to terrestrial habitats (Burton and Likens 1975; Gibbons et al. 2006), their declines warrant real concern for ecosystem managers.

The negative effects of urbanization on amphibians are numerous and extend beyond just habitat loss and fragmentation. Conversion of natural landscapes to urban cover can also lead to introductions of invasive species (Kiesecker 2003) and diseases (Carey et al. 2003), changes to the hydroperiod and water quality of breeding ponds (Casey et al. 2005; Rubbo and Kiesecker 2005) and altered amphibian behaviour due to noise and light pollution (Baker and Richardson 2006; Bee and Swanson 2007). Correspondingly, the vast majority of studies have reported a negative relationship between urbanization and amphibian species richness, abundance and diversity (as reviewed by Hamer and McDonnell 2008).

Despite a concerted effort to quantify the effect of urbanization on amphibians, they remain among the least-studied taxonomic groups in urban environments (Pickett et al. 2001; Hamer and McDonnell 2008). Especially lacking in the existing literature are studies that examine the behavioural response of amphibians to urbanization (McGarigal and Cushman 2002; Cushman 2006). Urban and suburban areas contain a variety of land-cover types that act as barriers to movement and represent low-quality habitat for amphibians (e.g. roads, buildings, lawn) (Dodd and Smith 2003; Gagné and Fahrig 2007). Thus, the movement behaviour of amphibians in urban environments is likely to be drastically different from that observed in pristine, “natural” systems. Understanding how urbanization affects habitat use and behaviour could lead to more effective management strategies for protecting amphibians in these environments (Cushman 2006; Birchfield and Deters 2005; Ramirez et al. 2012).

Canada’s population has nearly doubled since 1961 with a large proportion (81%) of its inhabitants now residing in urban areas (Statistics Canada 2011). The province of Alberta especially, has experienced extensive population growth and contains two of the country’s most rapidly expanding cities (Calgary and Edmonton). As urbanization is likely to continue in this region and throughout North America, studying amphibian populations that are currently affected by land-use change is the first step in creating conservation and management strategies to protect amphibian populations threatened by future urban expansion.

Study Area

The city of Edmonton is located within the aspen-parkland ecoregion of Alberta, which lies at the border between boreal mixedwood forests to the north and prairie grasslands to the south (Riley et al. 2007). Local climate is classified as semiarid with long cold winters, low precipitation and high evaporation (ESWG 1995). Native aspen parkland is largely dominated by grassland (predominately fescue and bentgrass species) and mixedwood forest stands with a large number of wetlands interspersed throughout (Hartley et al. 2007; Riley et al. 2007). Common tree species include trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*) and white spruce (*Picea glauca*). Forest stands in the parkland are also associated with a rich shrub understory consisting of beaked hazel (*Corylus cornuta*), red osier dogwood (*Cornus sericea*), choke cherry (*Prunus virginiana*) and willow (*Salix spp.*) among other species. The area surrounding Edmonton, and throughout the ecoregion, have been heavily impacted by human activity with an estimated 85-95% of native parkland lost to urbanization and agricultural practices (Alberta Environmental Protection 1997).

The landscape of Edmonton, a city of approximately 1.2 million people (Statistics Canada 2011), is mostly dominated by commercial and residential infrastructure but contains the largest urban park system in North America associated with the North Saskatchewan River and its watersheds (City of Edmonton, www.edmonton.ca). Three primary varieties of wetlands exist within the city: 1) upland stormwater ponds (constructed), 2) natural upland ponds and 3) natural oxbow ponds located in the city's river valley park system. Upland wetlands are classified as seasonal to permanent wetlands (Class III – V, Stewart and Kantrud 1971) with the majority maintaining open water throughout the growing season. Oxbow ponds in the river valley are also classified as seasonal to semi-permanent wetlands, with water levels recharging through rainfall and runoff throughout the summer.

Land-cover surrounding upland wetlands is generally characterized by a thin strip of unaltered, grassy riparian vegetation encircled by a mosaic of altered habitat (mowed grass, buildings, pavement, etc.) and residual patches of mixed-forest cover. Mixed forest cover dominates the ravine wetlands, although shrubby and grassy riparian areas exist at the water's edge. Previous studies have confirmed that all three varieties of wetlands are used as breeding habitat by amphibians in Edmonton (Scheffers 2010), including the wood frog (*Lithobates sylvaticus*), the focal species of my study.

Study Species

The wood frog is a pond-breeding amphibian found throughout much of North America. Its range extends from Alaska, through every province and territory of Canada and south into the US where it includes much of the northeastern and mid-eastern states (Russell and Bauer 2000). Adults are 30-60 mm when mature and are sexually dimorphic with females generally growing to larger sizes than males. Wood frogs are freeze-tolerant and will hibernate in terrestrial areas under leaf litter (Regosin et al. 2003). Following hibernation, adults emerge in early spring and migrate to nearby breeding pools, often seasonal or semi-permanent ponds, where calling and mating activity commence. In Alberta, breeding generally takes place from late April until early June, depending on location, and generally lasts for 1-2 weeks at any given pond (Russell and Bauer 2000).

After mating, adults leave breeding ponds and enter the surrounding terrestrial environment. Movement behaviour studies conducted in Maine and

Missouri found that wood frogs typically travel towards moist wooded habitats or stream edges, often selecting forest cover for travel during these migratory movements (deMaynadier and Hunter 1999; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007). Reported distances for migrations vary according to study system but generally average 100 m from breeding ponds, with maximum values as high as 340 m (Baldwin et al. 2006) and 350 m (Freidenfelds et al. 2011) recorded at breeding sites in Maine. Adults will predominately remain at summering grounds for the majority of the active season with return trips occurring in the fall, allowing individuals to overwinter closer to breeding ponds (Regosin et al. 2003; Baldwin et al. 2006; Blomquist and Hunter 2010). During terrestrial activity, frogs tend to select shaded habitat (often closed-canopy forest cover) associated with moisture-related ground cover (moss or leaf litter) (Constible et al. 2001; Baldwin et al. 2006; Rittenhouse et al. 2007).

Thesis Goals and Outline

The goal of my study was to document the movement behaviour and habitat use of a pond-breeding amphibian in an urban environment. I used radio telemetry to track wood frogs at 11 wetlands in the city of Edmonton, Alberta that were surround by varying levels of environmental disturbance and human development. In Chapter 2, I examine the post-breeding movement behaviour of adult wood frogs at both upland and ravine wetlands. I quantify movement rates and distances travelled from water for adults at study wetlands, and test for differences in these movement parameters between wetland types and between sexes. In addition, I examine the relationship between wood frog movement from breeding ponds and weather conditions, and the characteristics of land-cover surrounding the ponds, through the creation of empirically based models. The models also provide insight into the spatial scale at which adjacent land-cover best explains wood frog movement behaviour. In Chapter 3, I assess the post-breeding habitat use of wood frogs at multiple spatial scales. Specifically, I document home range sizes for tracked wood frogs and determine 2nd-order (selection of home range within population range), 3rd-order (selection of locations within home range) and micro- (selection of habitat within $1m^2$) habitat selection during the summer active period (May-Aug). Chapter 4 summarizes the main conclusions of my study and provides recommendations for conservation of wood frogs and other pond-breeding amphibians in urban environments.

Our knowledge of wood frog movement behaviour and habitat use is derived primarily from studies that have occurred in pristine habitat or habitats altered by forestry or agriculture practices. Very little is known about the post-breeding activity of wood frogs, or any anurans, in urban environments. My study aims to document wood frog migration distances from urban breeding ponds and identify important habitat features utilized by these animals during the summer active period. As the destruction and alteration of habitat in association with urbanization is inevitable, increased understanding of how amphibians utilize urban habitats could guide the design and protection of urban wetlands and associated terrestrial environments in the future.

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Chapter 2. Movement behaviour of adult wood frogs (*Lithobates sylvaticus*) at urban wetlands of Edmonton

Introduction

Due to a biphasic life history, many amphibians require both aquatic and terrestrial habitat to complete their life cycle. Adult amphibians utilize aquatic environments for reproduction (required for egg and larval development in many species), but will often spend much of their life in terrestrial environments (Semlitsch 2000). Many pond-breeding amphibians, including the wood frog (*Lithobates sylvaticus*), rely on terrestrial environments for migration, dispersal, foraging and overwintering, making these habitats important for the survival and persistence of populations (Semlitsch and Bodie 1998; Regosin et al. 2003; Homan et al. 2004; Baldwin et al. 2006). As overcrowding in areas immediately surrounding breeding ponds can lead to decreased growth, development rates and survival for individuals, amphibian populations rely on movement away from breeding ponds (dispersal and migration) to alleviate intraspecific competition (Harper and Semlitsch 2007; Berven 2009). With increasing habitat loss and fragmentation caused by human land-use, there are concerns that reduced connectivity between breeding ponds, reduced movement from breeding ponds and a lack of suitable terrestrial habitat will result in increased isolation of populations and population declines (Rittenhouse and Semlitsch 2007b; Semlitsch 2008).

Despite a variety of studies focused on amphibian movement in natural systems and systems managed for forestry, very little is known about amphibian movement and terrestrial habitat-use in urban environments. These environments are typically characterized by habitat fragmentation, low availability of native vegetation and a strong presence of “impermeable” landscape elements (mowed grass, pavement, human structures) and, as such, pose great challenges for amphibian populations reliant on terrestrial habitat (Gagné and Fahrig 2007; Hamer and McDonnell 2008). A growing body of work has begun to focus on the effects of urbanization on amphibian abundance and species richness (Hamer and McDonnell 2008; Hamer and Parris 2011; Banville and Bateman 2012; Scheffers et al. 2012), as well as the genetic consequences of fragmentation on urban amphibian populations (Noël et al. 2007; Crosby et al. 2009; Mikulicek and Pisut 2012). These studies often involve quantifying the level of urbanization surrounding ponds or wetlands and relating these measurements to amphibian abundance, presence or diversity.

Comparatively few studies have determined the post-breeding movement patterns and habitat use of amphibians in urban environments (but see Birchfield and Deters 2005; Husté et al. 2006; Paton et al. 2008; Ramirez et al. 2012). Many studies have provided evidence that the quality of terrestrial habitat surrounding breeding ponds is an extremely important factor in determining migration and dispersal behaviour in amphibians and ultimately the health and persistence of amphibian populations (e.g. deMaynadier and Hunter 1999; Semlitsch 2000; Semlitsch 2008). As urbanized landscapes are often associated with an abundance of lower-quality terrestrial habitat (habitat providing little shelter from predation, desiccation or foraging opportunities), it is likely that the dispersal and migration behaviour of amphibians breeding in these areas could be greatly affected. With increasing levels of urbanization and fragmentation occurring, it is important to identify how these types of land-use changes impact the movement ecology of pond-breeding amphibians (Vasconcelos and Calhoun 2004; Paton et al. 2008; Puglis and Boone 2012). Understanding how anurans and other amphibians travel through and use urban landscapes is a preliminary step in creating management and conservation strategies that allow freer movement by individuals and will presumably benefit amphibian populations affected by the pervasive threat of urbanization.

My study focuses on documenting the post-breeding movement patterns and habitat use of a pond-breeding anuran, the wood frog, in an urban landscape, and how land-cover and weather patterns affect these movement patterns. Specifically, I examined the movement rate and distances travelled from breeding ponds by adult wood frogs using radio tracking. Documenting how far wood frogs move from breeding ponds in an urban setting provides information on their migration capabilities and a basic estimate of the core area surrounding breeding wetlands that requires protection (Semlitsch 2000; Rittenhouse and Semlitsch 2007b). I included movement rate in my analysis as a proxy for habitat quality and landscape permeability (Isbell et al. 1998; Prange et al. 2004; Freidenfelds et al. 2011). My specific objectives were to (i) quantify the distances moved from water and movement rates (both important, commonly measured components of amphibian behaviour) of adult wood frogs through urban terrestrial habitat, (ii) determine the effect of land-cover surrounding urban wetlands on these movement parameters and (iii) examine other factors that may affect movement activity during the summer months, i.e., weather conditions and sex of tracked individuals.

To date, knowledge of terrestrial movement and habitat use of the wood frog has come from studies that have quantified these activities in either pristine, forested habitats or in habitats altered by forestry (e.g., clear-cut logging) or agriculture (Vasconcelos and Calhoun 2004; Baldwin et al. 2006; Freidenfelds et al. 2011; Rittenhouse and Semlitsch 2009). The majority of studies have focused on quantifying movement patterns for populations in the eastern and central United States (but see Bellis 1965; Constible et al. 2001; Okonkwo 2011). In these systems, following early spring (March-April) breeding activity at small ephemeral ponds, adult wood frogs migrate into terrestrial environments in search of summer foraging grounds (often moist forest habitat or damp, rocky drainages) which can also double as overwintering habitat (Regosin et al. 2005; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a). Migratory movements away from breeding ponds are often non-random in their orientation (adults exit a pond in the same place each year and travel towards appropriate terrestrial sites), occur over short time-spans (one day up to a few weeks) and are triggered by warm, wet weather (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007b; Semlitsch 2008). In studies using radio-telemetry and mark-recapture,, adult wood frogs have been located as far as 300 m (Vasconcelos and Calhoun 2004 – mark recapture), 340 m

(Baldwin et al. 2006 – radio telemetry), and 395 m (Rittenhouse and Semlitsch 2007a – radio telemetry) from their breeding ponds following migratory movements; however, the majority of individuals travel approximately 100 m from the ponds during the active season (Regosin et al. 2005; Rittenhouse and Semlitsch 2007b; Freidenfelds et al. 2011). During migration, wood frogs tend to select forested land-cover over more open, exposed conditions (fields or clearcuts) as closed-canopy habitats provide greater protection from desiccation (Gibbs 1998; Vasconcelos and Calhoun 2004; Rittenhouse and Semlitsch 2009). Although some studies have documented adult females migrating significantly greater distances from breeding ponds than males during the summer (Regosin et al. 2003), this difference is not reported in all populations (Rittenhouse and Semlitsch 2007b; Freidenfelds et al. 2011).

I predicted that wood frogs would travel greater distances from breeding wetlands in urban landscapes, compared to pristine systems, due to the high level of fragmentation of natural vegetation cover in the urban environment. Previous work documenting amphibian movement in areas with high fragmentation and habitat degradation surrounding the breeding ponds have shown that adults are forced to travel greater distances from their ponds in order to locate suitable summer foraging grounds (Husté al. 2006; Montieth and Paton 2006). I anticipated that males would remain closer to water and demonstrate lower movement rates during the active period compared to females based on results from previous studies (Regosin et al 2003; Rittenhouse and Semlitsch 2007a), including studies in fragmented habitat (Freidenfelds et al. 2011). Additionally, as wood frogs have been shown to prefer forested habitat over open, exposed habitat like grassland or agricultural land-cover (deMaynadier and Hunter 1999), I predicted that frogs at sites with greater coverage by woody vegetation (closed-canopy forest and shrub cover) would show lower rates of movement (more likely to remain longer in areas characterized by the shelter provided by trees and shrubs) but move farther from water over time than at sites supporting less natural cover (Freidenfelds et al. 2011).

Finally, I predicted that frogs would be more active (higher movement rates) and travel greater distances from water during periods of increased precipitation and higher temperatures. Weather conditions have been shown to be an important factor in determining the terrestrial movement of amphibians (Vasconcelos and Calhoun 2004; Baldwin et al. 2006; Rittenhouse et al. 2008), and Edmonton’s northern climate is predominately dry and cool (mean daily temperature for frog active period [May-October] = 12.8^{o}C) with little precipitation during the summer and fall (average total precipitation for May-October = 326mm (1981-2010; Environment Canada - http://climate.weather.gc.ca)).

Methods

Study Sites

Frogs were selected for radio-tracking from 11 wetlands within the city of Edmonton, located in the aspen parkland ecoregion of north-central Alberta, Canada (see Figure 2.1 for map of study wetlands). Sites were chosen based on confirmed wood frog presence in prior years (Scheffers 2010) and observed breeding activity (calling) in spring 2011. The mean distance between study wetlands was 8.3 ± 0.6 km (SE) (Range: 0.1 – 18.9 km). Of the 11 wetlands selected, seven were constructed stormwater ponds (average age = 11 years) located in upland residential and industrial developments. Edmonton's stormwater wetlands are permanent bodies of water designed to handle flooding and sequester pollutants from groundwater and surface runoff. The ponds varied in size (mean area =14 341 m^2, range = 3777 - 27 077 m^2) with surrounding terrestrial habitat consisting of a narrow band (mean width = 13.3 ± 2.7 m SE) of riparian vegetation encircled by a mosaic of altered habitat (mowed grass, houses, pavement, etc.) and patches of aspen-dominated forest. Dominant riparian vegetation included grasses, sedges, shrubs (*Salix spp.*, *Rosa acicularis* and *Cornus sericea*) and scattered trees (*Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera, Picea mariana* and *Picea glauca).* Three of the nine stormwater ponds contained one or more small islands (mean area = 3197.0 m^2, range: 125.8 - 6115.3 m^2) covered by vegetation similar to the riparian zones. In addition to the seven stormwater ponds, a natural upland wetland (Pond 308) was also included as a study site. Unlike the constructed stormwater ponds, this site existed as a natural, upland wetland prior to the construction of the housing development that presently surrounds it. The riparian zone of this pond closely resembled those of the stormwater ponds in its vegetation composition and width (8.26 m). The pond also contained an island composed of a thick layer of floating moss supporting tall (>3 m) shrubs (*Salix spp.*) and saplings (*Betula papyrifera*). Due to the high level of urbanization in the area, I had four upland wetlands that were “natural” and had detectible wood frog populations present. Despite conducting multiple foot searches throughout the frog active period and erecting drift fence arrays at these four wetlands, I was able to capture adult frogs large enough for radio tracking, at a singe wetland, Pond 308. Due to similarities between the natural Pond 308 and the seven constructed upland ponds (described above), I hereafter refer to all eight upland study wetlands as “upland ponds”. These eight ponds contained modest populations of wood frogs (average catch per unit effort (CPUE) from visual encounter searches = 1.09 adult wood frogs per hour searched) and at least one individual from each of the upland sites was tracked during 2011 and 2012.

Frogs were selected for tracking from three natural wetlands located in Whitemud Creek ravine. Ravine sites were permanent, slender oxbow ponds (average area = 4707 m^2, range: 3978 – 6111 m^2). The vegetation structure surrounding ponds consisted of a narrow riparian zone (mean width = 8.1 ± 1.9 m SE) surrounded by continuous boreal mixed-wood forest (*Populus tremuloides, Populus balsamifera*, *Betula papyrifera*, *Picea mariana* and *Picea glauca)*. Pond margins of ravine sites were more shaded than upland sites because of the proximity of forest stands and the topography of the ravine. All three ravine ponds contain large populations of wood frogs compared to the upland study sites (mean catch per unit effort (CPUE) from perimeter searches = 3.85 adults per hour searched) and multiple individuals were radio-tracked at each of the ponds during both 2011 and 2012 (see Appendix A for summary of pond characteristics and detailed count data).

Capturing and Tracking Wood Frogs

Wood frogs were captured for tracking during spring (late April and early May) and opportunistically throughout the summer in 2011 and 2012. Extensive searches on foot were conducted at all 11 study wetlands in April and May during and following breeding activity and also, less frequently, for the duration of the frogs' active season (May-October) to locate animals for tracking. All frogs were captured using dip nets or by hand and were held in shaded plastic buckets containing water until they were processed. In addition to visual searches, drift fence and pitfall trap arrays were used in 2012 at six of 11 wetlands to bolster the number of adults captured. Each captured frog was weighed, sexed and measured for snout-urostyle length (SUL). Following processing, all wood frogs weighing > 8.0 g were retained for radio-tracking whereas lighter individuals were immediately released within 5 m of the location of their capture. Less than 35% of all wood frogs captured exceeded the 8.0 g cut-off weight (mean weight of captured wood frog = 6.44 ± 0.22 g SE).

I used BD-2N transmitters weighing 0.4 g with a battery life of approximately 30 days (Holohil Systems Ltd., Carp, Ontario, Canada) to track wood frogs. Transmitters were attached using external waist belts composed of silicone tubing (outside diameter = 2.2 mm). Stretchy bead cord was threaded through the silicone tubing and the transmitter, and was used to cinch and tie down the belt. A belt sat just above the frog's pelvis with the transmitter resting on its back. Transmitter plus belts were always less than 10% of the frog's body weight (Richards et al. 1994). Following attachment, frogs were held in aquaria overnight to assess belt fit and to ensure movement was not impaired.

Frogs bearing radios were released within 5 m of their original capture site and relocated every 2-3 days (average = 2.2 days) using a Lotek Biotracker receiver (Lotek Wireless Ltd.) with attached three-element Yagi antenna. Individuals were tracked May-October in 2011 and May-September in 2012. Over the 2 years, I tracked 80 frogs (36 males and 44 females). Upon each relocation, a frog's GPS coordinates were recorded using either a Garmin GPSMAP 62s handheld unit (2011) or a Trimble GeoExplorer 3000 series (2012) and I categorized location by habitat type (i.e. forest, grass/low shrub, tall shrub etc., see below). Measurements of the straight-line distance to breeding pond (measured to closest shore), as well as distance from previous location, were recorded at this time using a tape measure when possible and GPS units when frogs had travelled large distances. Daily rainfall and temperature recordings were obtained from a nearby Environment Canada weather station (Edmonton City Centre AWOS) for both 2011 and 2012.

Geographic Information Systems Data

I created a land-cover geographic information systems (GIS) map of nine land-cover categories (see Table 2.1 for description of categories) from colour satellite images (map scale = 1:5000) taken in 2011 with 50-cm resolution (Source: DMTI Spatial) using ArcGIS 10.1 software package (Redlands, California). After each study wetland was digitized as a separate polygon, I digitized the terrestrial habitat surrounding each wetland, classifying terrestrial cover based on my selected land-cover categories.

I then created four different landscape buffers within the digitized terrestrial habitat surrounding each wetland. Buffers were created at distances of 10 m, 25 m, 50 m 100 m and 125 m from the ponds' edges. I chose to use a 10 m buffer and a 50 m buffer based on the mean distance from water travelled by frogs I tracked (~10 m) and the maximum distance travelled from any source of water by any tracked frog (~ 50 m) (see Results section for exact values). The 100 m buffer was chosen based on mean maximum distances moved from breeding ponds reported by other studies (Baldwin et al. 2006; Rittenhouse & Semlitsch 2007a, Freidenfelds et al. 2011). The 125 m buffer approximately represented the farthest distance any frog travelled away from a breeding pond. For each buffer size, the proportion of the total buffer area covered by each of the nine land-cover categories was quantified.

Analysis

Movement Parameters

Of the 80 adult wood frogs tracked in 2011 and 2012, only those individuals with five or more relocations were included in analyses (n = 50). I excluded relocation points where only detached transmitters were found in case a predator or scavenger had moved the transmitter. Three response variables were used to quantify frog movement patterns in terrestrial environments. For each individual animal, I calculated the mean distance travelled from the breeding pond's edge (DFBP; the straight-line distance that a frog was located from the nearest breeding pond edge averaged across all relocations) , the maximum distance from breeding pond travelled (MaxDFBP; greatest straight-line distance from the edge of a frog's breeding pond that it was ever located) and mean distance moved per day (DPD). A multivariate general linear model (GLM) was used to determine the effect of sex, tracking year and pond type (upland or ravine) on these three movement parameters. I included number of relocations recorded for each frog as a covariate to account for the disparity in length of tracking period among individuals. Preliminary models included Julian date to account for seasonal variation in behaviour, but this variable did not add to the explanatory power of models, and is excluded from GLMs presented here. A separate GLM was used to determine the effect of snout-urostyle length and weight at capture on movement parameters. All three response variables were log-transformed to meet assumptions of normality and homogeneity of variance.

Landscape Effect on Movement

For each landscape buffer (10 m, 25 m, 50 m, 100 m and 125 m) and for each pond, I incorporated the nine land-cover variables (Table 2.1) into a Principal Components Analysis (PCA) in order to consolidate landscape information. All ponds except pond 108, where tracking effort was insufficient, were included in the PCA. As land-cover data was continuous and the primary objective was to reduce the dimensionality of my correlated land-cover variables, PCA was chosen over other potential ordination techniques. Percentage cover for each of the land categories was transformed with a log ratio transformation in order to account for the unit sum constraint (Kucera and Malmgren 1998). Scores from the first three PC axes, which explained the majority of recorded variation in land-cover ($\geq$ 85% of combined variation explained), were used as the independent variables in linear mixed models to determine the effect of land-cover on the two parameters involving movement from breeding ponds (DFBP and MaxDFBP). By using PCA, instead of entering the cover categories directly into linear models, I avoided issues with highly correlated landscape variables. A separate set of models was generated for each of the movement parameters. In each mixed model, the two movement parameters were log-transformed to meet assumptions of normality and homogeneity of variance. A categorical variable, “pond type” (either upland or ravine), was included in half of the models to account for overall environmental differences frogs may have encountered when moving at upland, constructed ponds versus natural sites in the river valley (see Table 2.3 for a list of linear models and associated parameters). “Site” was included in each model as a random effect in order to account for the lack of independence among frogs tracked at the same study wetland. I used Akaike’s Information Criteria (AIC) to determine at which buffer distance the land-cover surrounding study wetlands best-explained wood frog movement patterns.

Delta AIC values corrected for small sample size (ΔAICc; Burnham and Anderson 2002) were used to compare candidate linear models. I considered the model with the lowest AIC value as the best model and any model with a ΔAICc < 2 to also have meaningful support (Burnham and Anderson 2002). Within each model, the effect of each coefficient on the response variable was determined by calculating a 95% confidence interval. If the 95% confidence interval did not overlap zero, this indicated a meaningful effect (either positive or negative). A coefficient was considered to have no meaningful effect if the 95% confidence intervals overlapped zero.

Weather Effect on Movement

Spearman ranked correlation tests were used to determine the effect of weather conditions (temperature and precipitation) on two movement parameters: straight line distance of a frog location to the nearest waterbody of any kind (DFW) (e.g., stream, pond) and movement rate (DPD) since last relocation. For each recorded frog location, the previous 48hrs were assessed for total precipitation levels and average temperature, using records collected at a centrally-located weather station. These values were then related to the two dependent variables (DPD and DFW) to determine the short-term effect of weather conditions on frog movement. All analyses were conducted using SPSS Ver. 20 (IBM Armonk, NJ) and R (R Foundation for Statistical Computing, Vienna, Austria).

Results

A total of 50 wood frogs with at least five locations were radio-tracked, 25 frogs in each year. An equal number of males (25) and females (25) were tracked across the 2 years and in total, 19 frogs were tracked at the ravine sites and 31 at the upland sites (six frogs at the natural upland wetland and 25 at the seven constructed wetlands) (Appendix B). On average, individuals were radio-tracked for 32.7 ± 2.9 days (mean ± SE) resulting in a total of 722 locations. Females were monitored longer (mean = 36.2 ± 4.5 days) than males (mean = 29.2 ± 3.5 days) but this difference was not statistically significant ($t_{28} = -1.21$, $P = 0.232$). Mean snout-urostyle length was 46.8 ± 0.6 mm (mean ± SE) and average body mass upon release was 11.9 ± 0.5 g (mean ± SE). Females (mean SUL = 49.4 ± 0.7 mm, mean weight = 13.5 ± 0.7 g) were, on average, larger than males (mean SUL = 44.5 ± 0.7 mm, mean weight = 10.2 ± 0.5 g).

In general, frogs remained very close to their breeding ponds throughout the active period. Contrary to previous studies of wood frog movement, there were few lengthy, post-breeding migratory movements into the terrestrial habitat during either year of tracking. Most frogs remained within the riparian zones of breeding wetlands (< 25 m from water) and only occasionally used adjacent upland habitat, during periods of increased precipitation, before returning to breeding-pond margins (mean DFBP = 12.8 ± 4.5 m SE; mean MaxDFBP = 26.7 ± 6.5 m SE). These short forays into the upland environments usually lasted 2-3 days before the frog returned to its home riparian zone. Of the 722 frog locations recorded, approximately 65% (n = 462) were within 5 m of the edge of the breeding pond. Preliminary analysis showed that neither weight nor body length had a significant effect on the three movement parameters.

Of the 50 frogs tracked over the two-year period, five individuals (four in 2011 and one in 2012) made one-way trips away from their breeding ponds, re-locating to terrestrial habitat beside streams or small pools of standing water. I viewed these individuals as “migrants” (Semlitsch 2008), as they never returned to their breeding ponds during the tracking period and distances travelled away from ponds were quite large (average MaxDFBP = 85.1 m) compared to the temporary movements from breeding ponds that were observed for the majority of my tracked frogs. All five migrant individuals were female and occurred at ravine wetlands where they bred before travelling through terrestrial habitat (typically forest) to reach their final destinations at stream or pond edges. Three of five individuals made migrations from breeding ponds during late May or early June and the remaining two during late July and early August. All occurred during or following periods of heavy rains.

Effect of Sex, Tracking Year and Wetland Type

Average values for DFBP, MaxDFBP and DPD (Figures 2.3, 2.4, 2.5; Appendix C) are summarized below. The number of relocations recorded did not have a significant effect on DPD ($P = 0.839$) or DFBP ($P = 0.486$), but did significantly affect MaxDFBP ($P = 0.044$) as frogs tracked for longer periods had larger recorded MaxDFBP values (one way ANOVA).

In general, DFBP measurements for females were greater than males and greater in 2011 compared to 2012, but these differences were not statistically significant (Sex: $F_{1,46}= 1.694$, $P = 0.200$; Year: $F_{1,46} = 0.318$, $P = 0.576$; – see Appendix C for average values). Pond type also had no effect on DFBP (Pond Type: $F_{1,46} = 1.377$, $P = 0.247$). Maximum distance travelled from breeding pond (MaxDFBP) tended to be greater for females than males, but again, differences were not statistically significant (Sex: $F_{1,46} = 2.487$, $P = 0.122$). MaxDFBP did not differ between the two sample years ($F_{1,46} = 0.772$, $P = 0.385$) or between the pond types ($F_{1,46} = 0.118$, $P = 0.735$).

Recorded values for distance per day (DPD) were very similar between the sexes ($F_{1,46} = 0.836$ $P = 0.366$) and did not differ between years ($F_{1,41} = 0.030$, P=0.862) or pond type ($F_{1,46} = 0.878$, $P = 0.354$) (Appendix C). All interaction effects between fixed factors (Pond Type, Year and Sex) were non-significant for the three movement parameters.

Land-cover and PCAs

Appendix D provides an overview of the land-cover present at the 11 study wetlands. Comparisons between sites at the largest buffer size (125 m) show distinct differences between the ravine and upland wetlands with regards to land-cover. Overall, the most common cover type at the eight upland wetlands was lawn/garden followed by pavement, and buildings. Tall shrub, bare ground and forest accounted for the lowest total area on the landscape. All upland study wetlands had some representation of each of the nine cover types except for Pond 404, which had no forest cover within its 125 m buffer. Ravine wetlands were largely dominated by forest cover but also had modest amounts of grass / low shrub, open water and tall shrub. Several land-cover categories were completely absent from the 125 m buffers around ravine wetlands; these included buildings, mowed grass and lawn/garden.

The first axis (PC1) of the PCA based on the nine land-cover types was positively correlated with the extent of buildings, pavement, lawn/garden, and mowed grass for the majority of spatial scales (10 – 125 m) and negatively correlated with forest cover and tall shrub (Table 2.2). No land-cover categories loaded consistently into PC2 or PC3 across spatial scales. Both PC2 and PC3 explained little variation in the land-cover data compared to PC1 (Table 2.2). A sample joint plot from the 50 m buffer land-cover PCA is shown in Figure 2.2. The ordination separated the study sites largely by their wetland type, with ravine ponds (310, 314 and 316) clustered in the top left and upland ponds mostly to the right. The two upland sites with abundant natural vegetation and large protected buffers (ponds 108 and 109) were located in the bottom left of the plot indicating that these sites more closely-resembled the natural ravine sites than the majority of upland sites in land-cover composition.

Relationship Between Land-cover and Movement Parameters

For both DFBP and MaxDFBP, Model 11 (pond type only) best explained the movements from breeding ponds for the tracked frogs (Table 2.4, 2.5). Of the models representing land-cover at various spatial scales, Model 5 (125m buffer) best explained DFBP and MaxDFBP (DFBP: ΔAIC = 4.10, MaxDFBP: ΔAIC = 5.01). Within the linear models, no coefficient estimate had a confidence interval that did not overlap zero, indicating that the PC scores (representing land-cover composition at the study wetlands) did not have a significant effect on the movement parameters analyzed. In general, the land-cover surrounding my study wetlands did not effectively predict the movements from breeding pond as even the top models (Model 11) explained very little overall variation in movements (DFBP; $R^2 = 0.03$, MaxDFBP; $R^2 = 0.01$).

Precipitation and Temperature

My results showed that precipitation levels ($r_s = 0.145$, $p = 0.006$, n = 722) and temperature ($r_s = 0.090$, $p = 0.016$) in the previous 48 h both had a significant, positive effect on a frog’s rate of movement (DPD) over that time period. Additionally, frogs were found farther from water (DFW) when temperatures had been higher in the 48 h prior to location ($r_s = 0.144$, $p < 0.001$) and when greater amounts of rain had fallen during that period ($r_s = 0.102$, $p = 0.006$).

Discussion

As urban landscapes are often associated with a variety of “impermeable” land-cover types (roads, mowed grass, buildings), movement and migration behaviour in amphibians and other wetland-associated species is likely altered in these areas compared to natural systems (Gagné and Fahrig 2007; Hamer and McDonnell 2008). Previous work on movement behaviour for amphibians and reptiles in urban areas have shown that migratory movements in landscapes impacted by human development are generally greater than those observed in natural environments (Montieth and Paton 2006 (spotted salamander, *Ambystoma maculatum*); Harden et al. 2009 (mud turtle, *Kinosternon subrurbrum*)), although the opposite has also been found for natterjack toads (*Epidalea calamita*, Husté et al. 2006). In general, radio-tracked frogs seemed largely confined to the habitat immediately surrounding breeding ponds as mean and maximum distances travelled from water were low compared to previously reported values during similar periods of the active season (spring and summer months immediately following breeding) (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a). Long-distance migratory movements away from breeding ponds were rare (only five of 50 frogs) and were observed only in females tracked at ravine study sites. A variety of factors including weather conditions, habitat quality and landscape features likely contributed to the movement patterns observed.

Short-term variation in the weather had a significant effect on the movement behaviour of tracked frogs. Wood frogs were located significantly farther from bodies of water and travelled greater distances between relocations when weather conditions were wet. Many amphibian species, including caudates (Roe and Grayson 2008; Veysey et al. 2009) and anurans (Bulger et al. 2003; Baldwin et al. 2006), rely on precipitation events to facilitate movement away from breeding ponds. Baldwin et al. (2006) found that wood frog movements within 24 hours following rainfall were significantly greater than movements with no rainfall, and movements were greater when temperatures were warmer. Movement in California red-legged frog (*Rana draytonii*) is also heavily tied to precipitation, as most frogs remain within 5m of ponds or streams throughout the summer months, only venturing into uplands during periods of rain (Bulger et al. 2003).

As anurans are prone to water-loss and face desiccation risks when travelling through upland habitat, precipitation can act as an important factor in determining when movement away from water bodies occurs (Pechmann and Semlitsch 1986; Todd and Winne 2006; Semlitsch 2008). Precipitation is even more important to anuran terrestrial movements in landscapes with high human-disturbance as these areas are often associated with lower humidity levels and less protective cover than pristine habitat (Mazerolle 2001; Chan-McLeod 2003). At wetlands in Edmonton, I found that frogs remained in very close proximity to their breeding ponds and only occasionally strayed from the ponds during or following periods of rain. This was especially pronounced at my upland wetland sites where frogs were almost always located within the unmowed buffer strips (mean width = 13.3 m) surrounding breeding ponds (424 of 469 locations recorded at upland wetlands) and were typically found beyond these boundaries only following precipitation.

Wood frog activity and movement has been shown to increase with higher ambient temperatures (Heatwole 1961; Vasconcelos and Calhoun 2004). As most amphibians primarily move through the terrestrial environment during night to avoid desiccation and predation, they are often most active during the coolest part of the day (Pechmann and Semlitsch 1986; Todd and Winne 2005). For most of the summer, temperatures at night in Edmonton likely would not limit movement (mean minimum daily temperatures for 2011 and 2012; June: 9.7 ^{o}C, July: 12.0 ^{o}C and August: 10.9 ^{o}C) but in May, shortly following the breeding season, mean night time temperatures were comparatively cool and potentially low enough to affect wood frog movement (mean minimum daily temperature = 5.1 ^{o}C).

Although my results indicate that precipitation and temperature patterns have a significant effect on short-term wood frog movements, there likely exist several other factors affecting movement behaviour. Desiccation risk (semi-permanent ponds often dry up during the summer), high adult densities leading to intraspecific competition for food resources at breeding ponds, and increased predation risk at pond margins are all considered important factors that trigger migration by wood frogs in the spring (Rittenhouse et al. 2009; Semlitsch 2008). In addition, desirable habitat for foraging and overwintering is often spatially distinct from habitat immediately surrounding the ponds (Rittenhouse and

Semlitsch 2007a; Freidenfelds et al. 2011) requiring frogs to travel through suboptimal terrestrial habitat to reach their final active-season destinations.

Following mating in spring, adult wood frogs have been reported to migrate away from breeding ponds, at times > 100 m, in search of summer foraging grounds and overwintering sites in adjacent terrestrial habitat (Regosin et al. 2005; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a). For example, in a telemetry study of wood frog movement at forested (mixed oak and pine) breeding ponds in Maine, Baldwin et al (2006) found that eight of 43 wood frogs made long-distance movements (mean distance = 192.5 m) and all tracked frogs left the breeding pond in search of upland habitat associated with moist forested wetlands or stream edges. Rittenhouse and Semlitsch (2007a) found that radio-tracked wood frogs in the oak-hickory forests of Missouri migrated from their breeding ponds (mean net distance travelled ≈ 110 m) to shaded, rocky drainages following rains in spring. At both study locations, wood frogs travelled significant distances from ephemeral ponds to moist, upland habitat (either wet forested areas or stream edges) where they remained for the duration of the tracking period. These "moisture islands" were identified as essential habitat in the terrestrial environment for wood frogs as they provided refuges from desiccation while also acting as good foraging sites due to high invertebrate activity (Regosin et al. 2005; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a).

Over two summers of observations, I documented only five long-distance movements away from breeding ponds at three of 11 study sites (mean maximum distance from water = 85.1 m). Although most wood frogs did make occasional forays into the upland habitat surrounding ponds, these trips were usually short in duration (2-3 days) with frogs largely remaining within 25 m of ponds before returning to the shore.

I believe that there are three primary factors driving differences in movement patterns between my study and patterns previously observed for wood frog. Firstly, the 11 wetlands included in my study are permanent waterbodies and provide constant refuge from desiccation throughout the summer. Thus, the benefits of remaining in close proximity to breeding wetlands could outweigh the costs of migration (energy consumption, risk of predation and desiccation) (Rittenhouse et al. 2009). Heatwole (1961), in a study of wood frogs at a Michigan wetland, also found that adults remained in close proximity to the pond's perimeter (< 1.0 m), maintaining their locations at the water's edge as the water-line receded. Only after the pond had fully dried did the frogs migrate into surrounding forested areas. One of the primary benefits of migration involves release from intraspecific competition at breeding wetlands (Semlitsch 2008; Rittenhouse et al. 2009). Information gathered from perimeter searches indicate that populations at my study sites were relatively low (mean upland adult CPUE per site = 1.09 frogs encountered per hour, range: 0.31 – 1.48), mean ravine adult CPUE = 3.85, range: 2.27 - 4.85) compared to natural upland wetlands in nearby Miquelon Lake Provincial Park (mean adult CPUE per site = 7.23, range = 0.36 - 27.4) (Anderson N. personal communication, 2013). As population sizes appear low at my study wetlands, competition for food and shelter are likely lower, thus reducing the need for frogs to migrate.

Secondly, distances from the continuous area of breeding wetlands to other moist habitat (streams, small wetlands) on the landscape were high at my upland sites where ponds were quite isolated. The mean distance from upland breeding pond edges to the closest stream or wetland was 222.5 ± 90.2 m (± SE, range: 38.4 – 876.4 m) and many of the breeding ponds were surrounded by a high proportion of human-altered habitat (Appendix D). As the average adult migration distances for wood frogs is approximately 100 m with maximum distances reaching as far as 395 m (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a; Freidenfelds et al. 2011), many of the upland breeding ponds included in my study were possibly too isolated from adjacent waterbodies that didn't hold breeding amphibians to allow for post-breeding migration. Additionally, wood frogs will generally avoid travelling through landscapes with little canopy cover and with high risk of desiccation and predation (Mazerolle and Desrochers 2005; Regosin et al. 2005). In a study of natterjack toad (*Epidalea calamita*) movement in an urban park in Paris, France, researchers reported minimal movement from breeding ponds and migration distances significantly smaller than those observed in natural systems (Husté et al. 2006). Exchanges of breeding adults between ponds within the park only took place when ponds were in close proximity to one another.

Compared to upland sites, ravine breeding ponds were closer to adjacent streams and wetlands (mean distance = 18.6 ± 1.7 m, ± SE, range = 15.5 – 22.6 m) and were also surrounded by significantly less disturbed land-cover (Appendix D). These conditions could explain why I only observed migratory movements at ravine wetlands and why, on average, frogs moved farther from breeding ponds (DFBP and MaxDFBP) at these sites than at upland sites (Appendix C).

Finally, differences in weather conditions between Edmonton and the study sites where previous tracking studies took place likely contribute to differences in movement patterns. Average precipitation totals for the months of May-August are much higher at the study sites in the US (Missouri: 434.3 mm and Maine: 335.5 mm) compared to Edmonton (272.5 mm) (Environment Canada 2013). As atmospheric moisture levels and the presence of moisture in the terrestrial environment have been identified as important factors driving the movement of adult and juvenile wood frogs (Heatwole 1961; Bellis 1962; Baldwin et al. 2006; Gravel et al. 2012), the amount and frequency of precipitation could affect wood frog movement from breeding ponds at my study sites (see discussion of short-term weather patterns above).

All five tracked individuals that demonstrated migration movements from ravine wetlands initiated the trips during or following periods of heavy rain and terminated migrations once they had reached habitat containing a body of water: a stream or small wetland. These findings suggest that frogs in our system are in fact capable of making migration movements away from their breeding ponds but only when alternative, wet landscape features are available and weather conditions are conducive to travel. All migrating individuals were female and were generally above average in size (average weight of migrants = 12.0 g, SUL = 47.7 mm). Previous studies have shown that female anurans tend to migrate farther from breeding ponds than males in search of higher-quality foraging patches on which to settle for the summer, which is believed to reflect higher energy requirements associated with egg production (Regosin et al. 2003; Rittenhouse and Semlitsch 2007b). As larger individuals are less vulnerable to desiccation due to their lower surface-area-to-volume ratio, larger wood frogs are also more likely to move through dry, exposed areas associated with higher desiccation risk (Bellis 1962; Chan-McLeod 2003; Mazerolle and Desrochers 2005). In my study system, males and smaller individuals may be less likely to attempt migration from breeding ponds as desiccation risks are high and male wood frogs gain a reproductive benefit from remaining close to breeding sites as they can arrive earlier following hibernation (Regosin et al. 2003; Rittenhouse and Semlitsch 2007b). Despite tracking several large females at upland wetlands, I observed no migration movements there. The combination of wetland isolation, high levels of human-altered land-cover and a lack of alternative and accessible water bodies surrounding upland wetlands all could be factors limiting migration movements for frogs at these sites.

Most wood frogs attempting migratory movements at my upland wetland sites would encounter swathes of human-modified land-cover (average width = 25.1 m) that separate breeding ponds from small forest patches or nearby waterbodies. Although some individuals tracked at upland sites did cross these inhospitable zones to reach forest or gardens (seven of 31 frogs), the majority remained within grassy riparian zones for the entire tracking period. The risks associated with travelling through mowed grass or other exposed land-cover may outweigh the benefits (release from intraspecific competition and locating higher-quality foraging patches) for tracked frogs at the upland study wetlands and discourage greater movements from water (Mazerolle and Desrochers 2005; Rittenhouse et al. 2009; Puglis and Boone 2012).

Four of the seven frogs that did move out of the grassy riparian zones of their upland breeding ponds were tracked at a single breeding pond (Pond 405) where the nearest forest patch was closer to the pond's edge (14.5 m) than any other upland site and, in some areas, the riparian zone grass transitioned directly into shrubby and then forest land-cover with no interruption by sections of human-modified land-cover. This unique situation could explain why I observed longer movements from the breeding pond at this site (mean MaxDFBP = 29.4 m) than for frogs tracked at any of the other upland wetlands (mean MaxDFBP = 11.1 m).

I predicted that the land-cover surrounding study ponds would have a significant effect on movement from breeding ponds as land-cover type and fragmentation have previously been identified as important factors in determining wood frog movement (deMaynadier and Hunter 1999 (Maine); Rittenhouse and Semlitsch 2009 (Missouri); Freidenfelds et al. 2011 (Maine)). My models indicated that land-cover alone did not effectively explain movements around breeding ponds at my study sites. Average (DFBP) and maximum distances moved from breeding ponds (MaxDFBP) were best explained by the "pond type only" model, but even the top models explained little variation in movements (DFBP- $R^2 = 0.03$; MaxDFBP - $R^2 = 0.01$). As land-cover composition did not accurately predict movements from breeding ponds, it is possible that factors like landscape configuration, connectivity and fragmentation are more important in influencing the movement behaviour of wood frogs in Edmonton (see also Mazerolle and Desrochers 2005; Fortin et al. 2012). Apart from a pair of exceptions (Ponds 108 and 109) the “pond type” description of study wetlands seemed to effectively integrate differences in land-cover composition at my breeding ponds (Figure 2.2). Despite obvious differences in land-cover composition between upland and ravine wetlands, I did not observe significant differences in the movement behaviour of frogs tracked at the two pond types. Apparent low levels of intraspecific competition present at study wetlands and permanent waterbodies both could have led to the similar movement patterns that I observed at both upland and ravine ponds.

Conclusions

Many pond-breeding amphibians, including the wood frog, rely on terrestrial environments for migration, dispersal, foraging and overwintering, making these habitats important for the survival and persistence of populations. As anthropogenic habitat destruction and degradation continues to be one of the greatest threats to amphibian diversity worldwide (Stuart et al. 2004), understanding how amphibians move in a landscape heavily altered by human disturbance is important for predicting how population persistence may be affected by these kinds of land-use changes. My study provides preliminary insights into the post-breeding movement behaviour of a forest-associated anuran species at urban wetlands. Their potential for informing decisions on urban wetland management will be further discussed in Chapter 4.

Tables and Figures

Table 2.1 Classification of land-cover types in the digitized zone surrounding 11 urban wetlands of Edmonton, Alberta.

Land-cover	Description
Pavement	Paved surface (road or sidewalk) often associated with high human and automobile traffic
Mowed Grass	City-maintained grass surface, mowed several times throughout the year
Lawn/Garden	Mix of mowed grass and planted gardens (front and back yards associated with houses)
Building	House or other building
Water	Open water
Grass/Low Shrub	Unmowed graminoids and low-lying shrubs (< 3.0 m in height)
Forest	Land-cover dominated by trees (either deciduous, coniferous or mixed-wood stands) with distinct canopy visible on air photos
Tall Shrub	Shrub cover (often *Salix spp.*) greater than 3.0 m in height
Bare Ground	Unvegetated soil (e.g. sandy washout near stream, undeveloped residential lot, gravel walking paths)

Table 2.2 Results of Principal Components Analysis using the proportion of nine land-cover variables at four increasing buffer sizes (Scale = buffer diameter) around 10 study wetlands in Edmonton, Alberta. I present land-cover variables that showed high ($R^2 > 0.6$) correlations with site scores on the first three principal component axes (PC1, PC2 and PC3) and whether variables were positively (+) or negatively (-) correlated with the axes. The amount of variation explained by each principal component axis (1-3) is also listed.

Scale (m)	**PC1 Variables**	**% Variance Explained**	**PC2 Variable**	**% Variance Explained**	**PC3 Variable**	**% Variance Explained**
10	Lawn/ Garden (+) Forest (-) Mowed (+)	50	Bare Ground(-)	22		12
25	Building (+) Lawn/ Garden (+) Water (+) Forest (-) Bare Ground (-) Mowed (+) Tall Shrub (-)	67		15		8
50	Pavement (+) Building (+) Lawn/ Garden (+) Water (+) Forest (-) Bare Ground (-) Mowed (+) Tall Shrub (-)	77		9		6
100	Pavement (+) Building (+) Lawn/ Garden (+) Mowed (+) Forest (-)	80		8		6

Table 2.2 Continued on P. 42

Table 2.2 Continued.

	Tall Shrub (-) Bare Ground (-) Grass/ Low Shrub (-)					
125	Pavement (+) Building (+) Lawn/ Garden (+) Mowed (+) Water (-) Tall Shrub (-) Bare Ground (-) Grass/ Low Shrub (-)	81		8		4

Table 2.3 List of fixed factors entered into the candidate mixed linear models used in AIC analysis. All models included "Site" as a random effect. PC1, PC2 and PC3 represent the scores assigned to each study wetland based on how their land-cover loaded onto the first, second and third PC axes, respectively, for each buffer size. PC1-10m represents the PC scores assigned to each wetland according to how the land-cover within 10m of the breeding pond loaded along PC axis 1. The "Pond Type" variable indicates whether the pond was a ravine pond or an upland pond.

Model	Included Parameters	Number of Parameters (*k*)
1	PC1-10m, PC2-10m, PC3-10m	3
2	PC1-25m, PC2-25m, PC3-25m	3
3	PC1-50m, PC2-50m, PC3-50m	3
4	PC1-100m, PC2-100m, PC3-100m	3
5	PC1-120m, PC2-120m, PC3-120m	3
6	PC1-10m, PC2-10m, PC3-10m, Pond Type	4
7	PC1-25m, PC2-25m, PC3-25m, Pond Type	4
8	PC1-50m, PC2-50m, PC3-50m, Pond Type	4
9	PCA1-100m, PCA2-100m, PCA3-100m, Pond Type	4
10	PC1-120m, PC2-120m, PC3-120m, Pond Type	4
11	Pond Type	1

Table 2.4 Mixed linear models with associated coefficients (land-cover PC scores and pond type) testing the effect of land-cover on average movement from breeding pond (DFBP*) by wood frogs. For each coefficient entered into a model, a parameter estimate is listed as well as whether the estimate had a positive or negative (+/-) effect on the response variable. Significance and direction of coefficient effects were determined using confidence intervals. If the 95% confidence interval did not overlap zero, the coefficient was considered to have a meaningful effect on the response variable and the direction of the relationship is indicated (either + or -). Coefficients with an overall weak effect on the responding variable (confidence interval overlaps zero) are marked with 'NA'. AICc and ΔAICc values are used to compare the various models and determine which buffer size was most important in determining DFBP. The most parsimonious model is indicated by 'Φ'.

Model	PC1 Coeff	+/-	PC2 Coeff	+/-	PC3 Coeff	+/-	Pond Type	+/-	AICc	ΔAICc
1	.1098	NA	.0232	NA	.0209	NA	X	X	121.31	9.16
2	.0600	NA	.0328	NA	.2610	NA	X	X	120.36	8.21
3	.0564	NA	.0727	NA	.2032	NA	X	X	121.22	9.07
4	.0540	NA	.1646	NA	.2440	NA	X	X	119.86	7.71
5	.0291	NA	.1032	NA	.5363	NA	X	X	116.25	4.10
6	.1036	NA	.0239	NA	.0369	NA	.0613	NA	123.33	11.18
7	.0548	NA	.0463	NA	.2461	NA	.0922	NA	122.72	10.57
8	.0401	NA	.0622	NA	.2649	NA	.2543	NA	122.92	10.77
9	.0352	NA	.1646	NA	.2965	NA	.2754	NA	121.57	9.42
10	.0199	NA	.1090	NA	.5192	NA	.1381	NA	119.08	6.93
11	X	X	X	X	X	X	.2223	NA	112.15	0 Φ

* DFBP = the straight-line distance that a frog was located from the nearest breeding pond edge averaged across all relocations

Table 2.5 Mixed linear models with associated coefficients (land-cover PC scores and pond type) testing the effect of land-cover on average movement from breeding pond (MaxDFBP*) by wood frogs. For each coefficient entered into a model, a parameter estimate is listed as well as whether the estimate had a positive or negative (+/-) effect on the response variable. Significance and direction of coefficient effects were determined using confidence intervals. If the 95% confidence interval did not overlap zero, the coefficient was considered to have a meaningful effect on the response variable and the direction of the relationship is indicated (either + or -). Coefficients with an overall weak effect on the responding variable (confidence interval overlaps zero) are marked with 'NA'. AICc and ΔAICc values are used to compare the various models and determine which buffer size was most important in determining MaxDFBP. The most parsimonious model is indicated by 'Φ'.

Model	PC1 Coeff	+/-	PC2 Coeff	+/-	PC3 Coeff	+/-	Pond Type	+/-	AICc	ΔAICc
1	.0792	NA	.0162	NA	.0561	NA	X	X	98.48	9.34
2	.0559	NA	.0584	NA	.1471	NA	X	X	97.51	8.37
3	.0465	NA	.0391	NA	.1822	NA	X	X	98.38	9.24
4	.0427	NA	.0865	NA	.1925	NA	X	X	96.88	7.74
5	.0258	NA	.0603	NA	.3385	NA	X	X	94.15	5.01
6	.0777	NA	.0171	NA	.0594	NA	.0119	NA	101.69	12.55
7	.0551	NA	.0612	NA	.1450	NA	.0164	NA	101.05	11.91
8	.0411	NA	.0350	NA	.2028	NA	.0851	NA	101.70	12.56
9	.0360	NA	.0871	NA	.2097	NA	.0975	NA	100.21	11.07
10	.0256	NA	.0604	NA	.3381	NA	.0029	NA	97.89	8.75
11	X	X	X	X	X	X	.1135	NA	89.14	0 Φ

* MaxDFBP = greatest straight-line distance from the edge of a frog's breeding pond that it was ever located

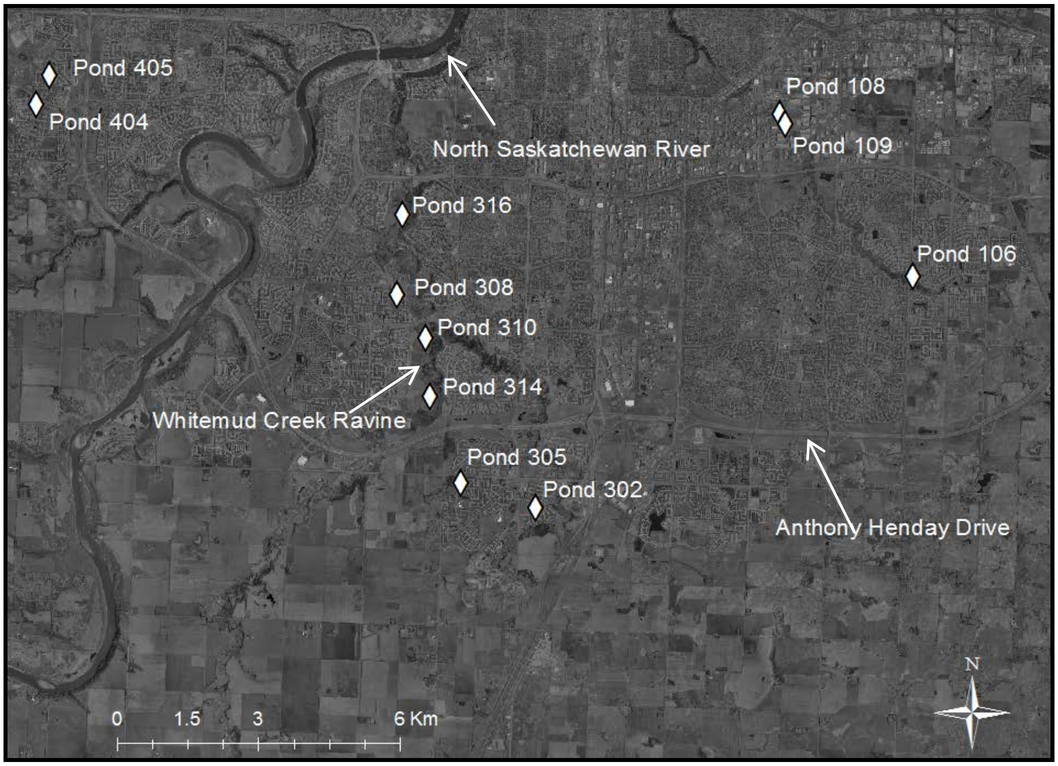

Figure 2.1 Map of Edmonton, Alberta showing 11 study wetlands where radio tracking took place.

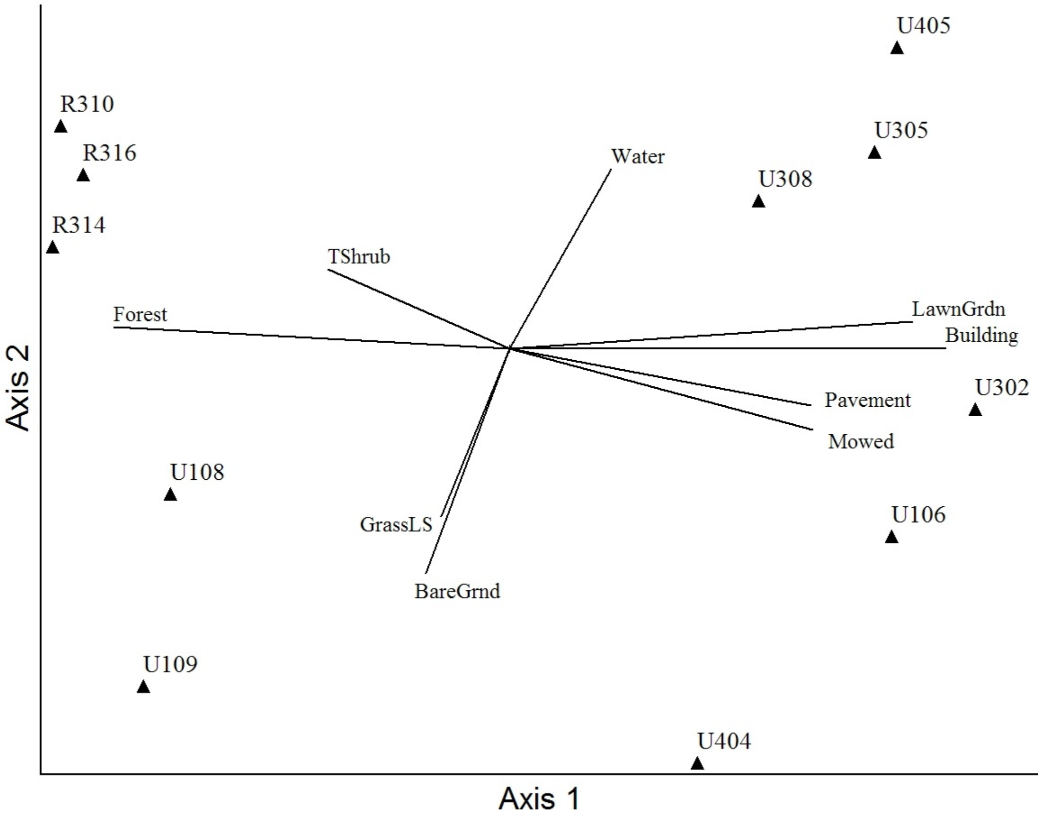

Figure 2.2 Principle components analysis (PCA) joint plot of land-cover within 50 m buffers at 10 study wetlands. Vectors point in the direction of increased coverage of various land-cover categories and length of vectors indicate the strength of the relationship. Study wetlands (represented by triangles) are arranged in multidimensional space according to their composition of land-cover. Land-cover categories include; water, tall shrub (TShrub), forest, grass/low shrub (GrassLS), bare ground (BareGrnd), lawn/garden (LawnGrdn), buildings, pavement and mowed grass (Mowed) (see Table 2.1 for detailed description of cover categories). Ponds are labeled by their pond type; either upland (U) or ravine (R).

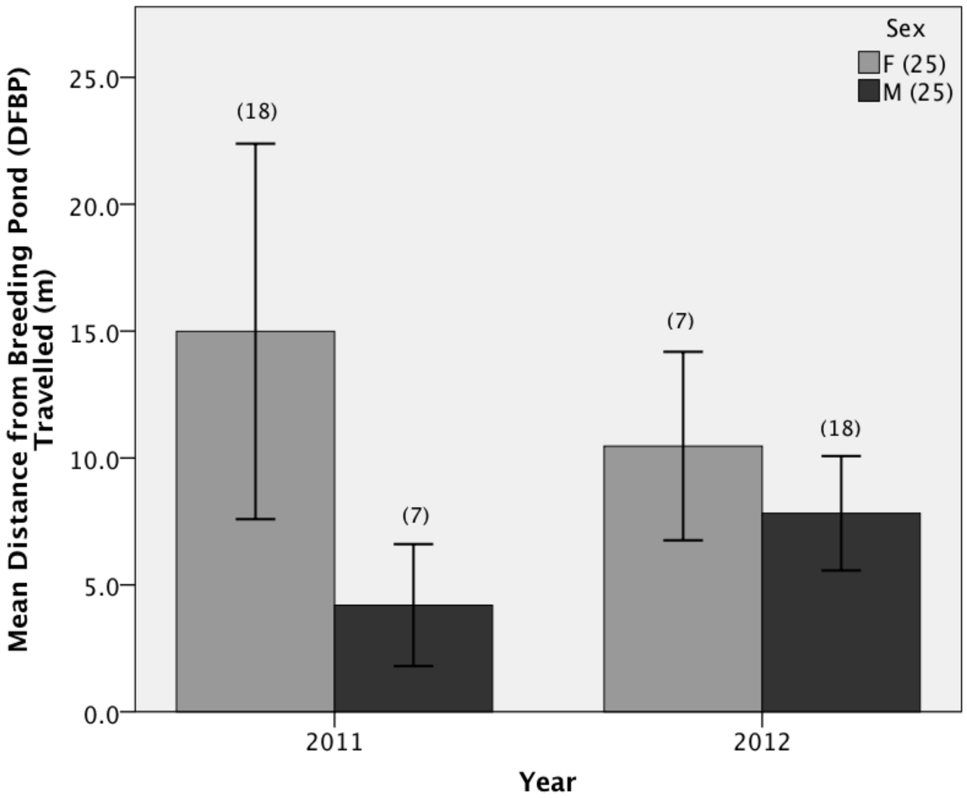

Figure 2.3 Mean distance travelled from breeding pond (DFBP) as a function of sex and tracking year for 50 wood frogs at 11 urban wetlands of Edmonton, Alberta. Confidence intervals represent +/- 1 SE and sample sizes are provided in parentheses.

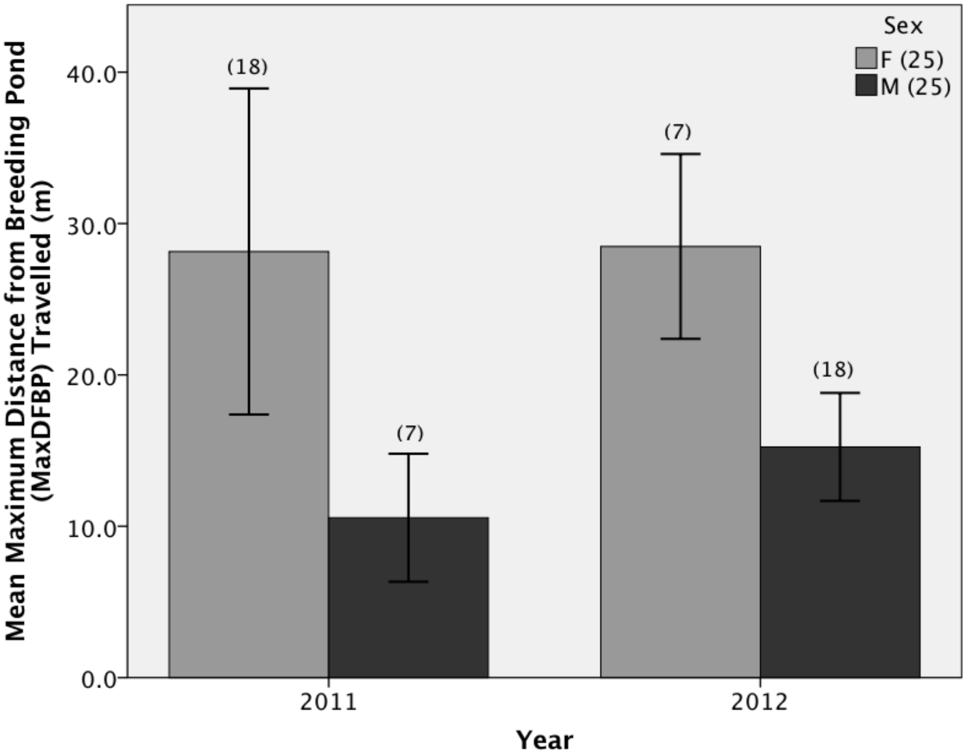

Figure 2.4 Mean maximum distance from breeding pond travelled (MaxDFBP) as a function of sex and tracking year for 50 wood frogs at 11 urban wetlands of Edmonton, Alberta. Confidence intervals represent +/- 1 SE and sample sizes are provided in parentheses.

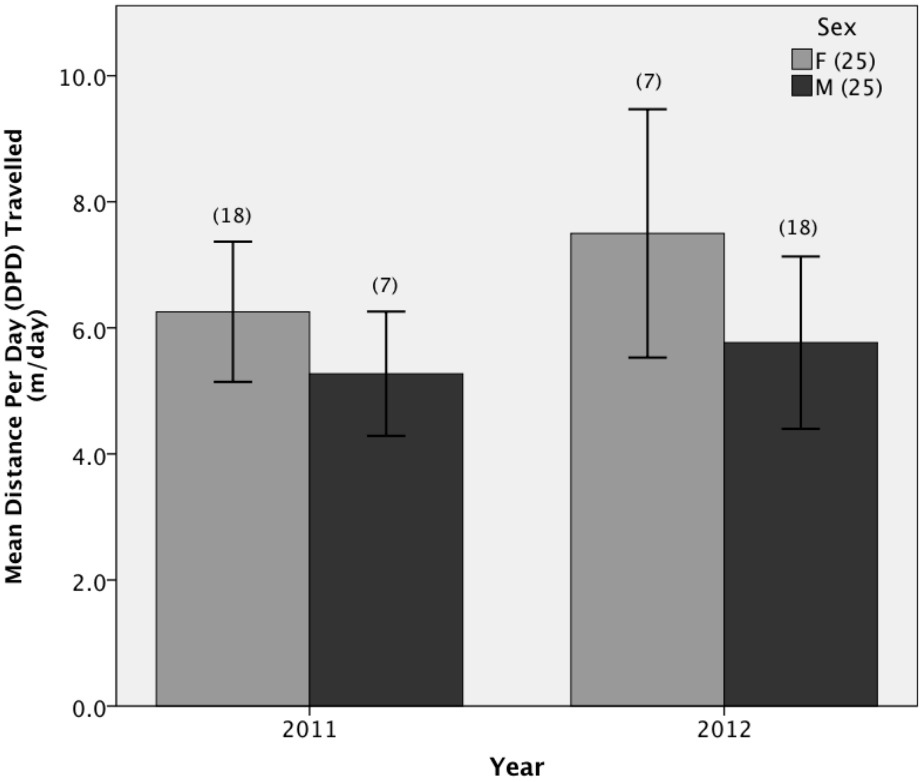

Figure 2.5 Mean distance travelled per day (DPD) as a function of sex and tracking year for 50 wood frogs at 11 urban wetlands of Edmonton, Alberta. Confidence intervals represent +/- 1 SE and sample sizes are provided in parentheses.

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Chapter 3. Multiscale habitat use and home range size of adult wood frogs tracked at urban wetlands.

Introduction

Understanding the distribution of species in the environment and how they utilize available resources is central to ecology. Habitat selection occurs when an individual uses a certain resource disproportionately to that resource's availability in the environment (Johnson 1980). Ideally, a species' habitat selection should be quantified at multiple spatial scales (hierarchical approach) as selection at a particular spatial scale is dependent upon selection at the scale one step higher in the hierarchy (e.g. selection of home range is dependent upon selection of population range; Johnson 1980; Alldredge and Griswold 2006; Edge et al. 2010). Investigations of a species' habitat use at multiple spatial scales are more likely to produce biologically meaningful results by avoiding the biases inherent in choosing a single spatial scale at which to quantify habitat use.

Habitat selection in degraded or fragmented landscapes can be quite different from habitat selection in pristine environments because, pristine environments often contain large tracts of high-quality habitat for a resident species with few unusable patches present on the landscape (Alldredge and Griswold 2006; Edge et al. 2010). In contrast, high-quality habitat patches may be rare in fragmented landscapes and isolated by large areas of matrix habitat as a product of land-use changes due to human activities. As a result, habitat selection for a species would be more likely to be detectible in these environments as only some habitats are capable of satisfying a species' requirements to exist in the area (Boyce and McDonald 1999; Alldredge and Griswold 2006). It is important to understand if and how a species' preference for certain habitat types differs with varying levels of environmental disturbance in order to improve conservation planning and management for wildlife facing increasing pressure from urbanization and other human-related disturbances.

Habitat loss and fragmentation caused by urbanization are considered to be among the greatest threats to amphibian populations worldwide (Stuart et al. 2004; Baillie et al. 2004; Hamer and McDonnell 2008). Many amphibians rely not only on aquatic environments for breeding, but also terrestrial environments for post-breeding dispersal and foraging. Consequently, amphibian populations existing in fragmented landscapes caused by urbanization could experience reduced dispersal capabilities, population isolation and even local extinction (Smith and Green 2005; Gagné and Fahrig 2007; Semlitsch 2008). Urban environments pose additional risks to amphibian populations in the form of direct mortality due to roads and increased abundance of human-subsidized predators such as domestic cats (*Felis catus*) (Woods et al. 2003; Harden et al. 2009; Jackson and Fahrig 2011). Due to the negative impacts of urbanization on amphibian populations and the ever-increasing rate of habitat destruction and fragmentation, it is important to create strategies to conserve and protect amphibian populations located in areas affected by anthropogenic land-use changes. One component of creating an effective conservation strategy for urban amphibians is to identify terrestrial habitats utilized by these animals in cities (Hamer and McDonnell 2008; Scheffers and Paszkowski 2012).

To date, the majority of our knowledge of terrestrial habitat use and selection by amphibians has come from studies conducted in either pristine environments or those altered by forestry or agricultural practices (deMaynadier and Hunter 1999; Constible et al. 2001; Rothermel and Semlitsch 2002; Baldwin et al. 2006; Gagné and Fahrig 2007; Rittenhouse and Semlitsch 2007a). Despite a growing body of work focused on the consequences of urbanization on amphibian abundance (Banville and Bateman 2012; Scheffers et al. 2012), community species richness (Hamer and Parris 2011) and the genetic structure of populations (Noël et al. 2007; Crosby et al. 2009; Mikulicek and Pisut 2012), very few studies have attempted to quantify habitat use and selection of amphibians in urban environments (but see Birchfield and Deters 2005; Puglis and Boone 2012; Ramirez et al. 2012). The handful of studies that have quantified urban amphibian habitat-use predominately focus on microhabitat selection, are generally short in duration and mostly address a narrow component of terrestrial habitat use (e.g. an animal’s preference between mowed or un-mowed grass; Puglis and Boone 2012; Ramierz et al. 2012).

In this study, I use radio-telemetry to model wood frog terrestrial habitat use at multiple spatial scales within an urban environment. Quantifying wood frog habitat use at multiple spatial scales and over a greater temporal scale (summer active period) will contribute to a general understanding of how pond-breeding amphibians select habitat in an urbanized landscape. The wood frog is a pond-breeding, forest-associated species which, due to its wide geographic range and similar terrestrial habitat requirements to other forest-associated amphibians (e.g. spotted salamander, *Ambystoma maculatum*, marbled salamander, *Ambystoma opacum* and green frog, *Rana clamitans*), offers an effective model for quantifying amphibian habitat use in a human-dominated landscape (deMaynadier and Hunter 1999; Rothermel and Semlitsch 2002; Todd et al. 2009). Information on specific behaviours, like habitat use and movement patterns, in a model species like the wood frog could ultimately provide insight into what makes various amphibian populations more or less susceptible to urbanization and could also identify landscape features that promote or hinder the persistence of amphibian populations (Puglis and Boone 2012; Scheffers and Paszkowski 2012).

Adult wood frogs, following mating activity in the spring, rely primarily on forested and occasionally grassland habitat for dispersal/migration, summer foraging areas and overwintering (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a). Previous studies in Maine and Missouri, USA that have quantified habitat use at a landscape scale have found that wood frogs prefer closed-canopy forests to “open” land-cover (grassland or forestry cut-blocks) and generally migrate from their breeding ponds towards moist, forested wetlands or stream edges where they will spend the remainder of their active period (deMaynadier and Hunter 1999; Baldwin et al. 2006; Rittenhouse and Semlitsch 2009; Okonkwo 2011). Since habitat fragmentation and destruction are commonly associated with urban areas, the availability of suitable habitat for wood frog migration, foraging and overwintering in urbanized landscapes is likely drastically different from the environments in which previous habitat-use studies have taken place. Urban landscapes are often associated with small, isolated and poorly-connected forest patches (Gagné and Fahrig 2007) which could be inaccessible to frogs during the active period due to spatial isolation from breeding wetlands and the presence of inhospitable urban land-cover features (i.e. pavement, mowed grass etc.) (Mazerolle 2001; Ramirez et al. 2012). The potential lack of quality habitat (that which provides shelter from predation and desiccation during upland activity) and the inability to access what quality habitat does exist, could affect how wood frogs use habitat in urban environments (Alldredge and Griswold 2006; Edge et al. 2010).

I investigated macrohabitat and microhabitat selection as well as determined home range size for wood frogs in Edmonton, Alberta's urban wetlands using radio-tracking. Macrohabitat selection was quantified over two field seasons (2011 and 2012) and at two spatial scales (selection of home range within population range and selection of locations within home range) whereas microhabitat was studied at one spatial scale (habitat within $1m^2$ of individual frog locations) and over a single field season (2012). As anurans and other amphibians face the risk of desiccation when using upland habitat, most individuals will select microhabitat that reduces water loss (Rittenhouse et al. 2008). Accordingly, I predicted that wood frogs would select microhabitat with higher coverage of leaf litter (which traps and maintains soil moisture), bryophytes (a ground cover associated with high moisture conditions) and lower light levels (evaporative water loss is reduced in shaded areas).

Macrohabitat selection is an extension of frogs' selection of microhabitats as they are physiologically tied to microhabitats that provide opportunities to thermoregulate and reduce water loss (Seebacher and Alford 2002; Rittenhouse et al. 2008) and thus, macrohabitats that support these conditions. I predicted that frogs would be located in and nearby tall shrub and treed areas that form a closed canopy as both habitat features provide shade and contain significant amounts of leaf litter at ground level. As lawns and pavement provide little shelter for wood frogs, I predicted that tracked individuals would be located farther from these cover types than expected based on availability on the landscape. Wood frog movements at urban wetlands in Edmonton (especially those located upland) were largely constrained to the habitat immediately surrounding their breeding wetlands, with few individuals moving beyond the grassy riparian zones of ponds (Chapter 2). Therefore I expected that grass and low shrub cover would be significantly selected for despite being relatively rare on the landscape compared to other cover classes. This cover type was often in close proximity to water, providing osmoregulatory opportunities for frogs, and would also contain variable light levels which frogs could exploit to accommodate their thermoregulatory needs (Seebacher and Alford 2002; Bartelt et al. 2004).

To my knowledge, no peer-reviewed study has used radio telemetry to quantify anuran habitat use in an urban environment or studied urban amphibian habitat use at multiple spatial scales. I hope to provide preliminary insight into how a forest-associated anuran uses the terrestrial habitat surrounding urban breeding ponds. Documenting the selection or avoidance of specific land-cover features by wood frogs could provide information on how urban wetlands can be designed and managed in order to ensure that the habitat requirements of this species are being met.

Methods

Study Sites

Frogs were selected for radio-tracking from 11 wetlands within the City of Edmonton, located in the aspen parkland ecoregion of north-central Alberta, Canada. Sites were chosen based on confirmed wood frog presence in prior years (Scheffers 2010) and observed breeding activity (calling) in spring 2011. The average distance between study wetlands was 8.3 ± 0.6 km (SE) (Range: 0.1 – 18.9 km).

Of the 11 wetlands selected, seven were constructed stormwater ponds (average age = 11 years) and one was a natural pond located in a housing development. The remaining three wetlands were natural oxbow ponds situated in the Whitemud Creek Ravine, part of Edmonton’s river valley park system. The upland ponds were of variable size (average = 14 341 m^2, range = 3777 – 27 077 m^2) with adjacent upland habitat consisting of a narrow band (average width =13.3 ± 2.7m SE) of riparian vegetation encircled by a mosaic of altered habitat (mowed grass, buildings, pavement, etc.) and patches of residual mixed-forest cover. The natural ravine ponds were generally smaller in size than upland ponds (average area = 4707 m^2, range: 3978 – 6111 m^2). Vegetation structure was characterized by a narrow riparian zone (average = 8.1 ± 1.9 m, SE) surrounded predominately by boreal mixed-wood forest (*Populus tremuloides*, *Populus balsamifera, Betula papyrifera, Picea mariana* and *Picea glauca).* Riparian vegetation at both upland and ravine wetlands included grasses, sedges, shrubs (*Salix spp.*, *Rosa acicularis* and *Cornus sericea*) and scattered trees.

Capture and Radio Tracking

Wood frogs were captured at breeding ponds for radio-tracking during spring (late April and early May) and opportunistically throughout summer in 2011 and 2012. Each captured frog was weighed, sexed and measured for snout-urostyle length (SUL). Following processing, all wood frogs weighing > 8.0 g were retained for radio-tracking while lighter individuals were released within 5 m of their capture location. I used BD-2N transmitters (Holohil Systems Ltd., Carp. Ontario, Canada) weighing 0.4 g with a battery life of approximately 30 days for tracking. Transmitters were attached using external waist belts composed of silicone tubing (outside diameter = 2.2 mm). Stretchy bead cord was threaded through both the silicone tubing and the transmitter, and was used to cinch and tie down the belt at the frog’s pelvis. Following attachment, frogs were held in aquaria overnight to assess belt fit and to ensure movement was not impaired.

Frogs bearing transmitters were released within 5 m of their original capture site and relocated every 2-3 days (average = 2.2 days) using a Lotek Biotracker receiver (Lotek Wireless Ltd.) with attached three-element Yagi antenna. Individuals were tracked May-October in 2011 and from May-September in 2012. Upon each relocation, the frog’s GPS coordinates were recorded using either a Garmin GPSMAP 62s handheld unit (2011) or a Trimble GeoExplorer 3000 series (2012). In addition to recording measurements of distance to breeding pond and distance from previous location with a handheld GPS or measuring tape, habitat information was collected for each frog.

Habitat Measurements

I collected habitat use information at two different spatial scales; microhabitat and macrohabitat. To determine macrohabitat use, the terrestrial habitat surrounding the 11 study wetlands was digitized using aerial photos and classified into nine different land-cover categories (see Chapter 2 methods for full description of the digitizing process; land-cover categories are listed in Table 3.1). Each frog location (both tracking years) was assigned to one of the cover categories based on the digitized images. To reduce spatial autocorrelation, habitat information was only collected for locations that were at least 1 m away from the frog’s previous location.

In 2012, I also collected microhabitat information from a 1-m^2 quadrat centred on a frog’s location. Microhabitat variables were chosen for collection based on previous habitat-use studies for wood frogs (Constible et al. 2001; Baldwin et al. 2006), as well as variables that I deemed to be biologically important for the species. Only locations at least 1 m from the previous location were sampled and only terrestrial relocations were assessed for microhabitat information (i.e., locations in water were excluded). At each location, I visually estimated the percentage of the quadrat occupied by each cover type (e.g. grass, leaf litter, shrub), quantified abiotic parameters (e.g. soil moisture, light transmission), measured average height of vegetation, and recorded distance to closest standing water (see Table 3.2 for full list of microhabitat measurements). Light levels were taken in the middle of the plot at ground level using a light meter (General Electric, Type 217). I then divided the plot's light level by the ambient light level (collected at ground level from an area with no overhead vegetation cover, i.e. pavement, mowed grass) to determine proportion of available light transmission for the plot. Soil moisture was collected at the northeast corner of the quadrat using a Kelway soil moisture reader (Model HB-2). Height measurements for grasses, forbs, and shrubs were taken at each of the four corners of the 1-m^2 quadrat and then averaged. I measured the height of the individual stems closest to the corners for each category listed above.

To document microhabitat availability, each frog-location plot was paired with a corresponding random plot of equal size in which I measured the same microhabitat parameters collected at the frog's location. Random plots were placed 5 m from the frog point in a randomly-selected compass bearing. The 5 m distance was based on the mean distance between successive frog locations recorded during tracking in 2011.

Habitat Selection Analysis

Macrohabitat selection for tracked wood frogs was analyzed at two spatial scales; 2nd order (selection of individual home ranges within the population range) and 3rd order (selection of locations within the home range) (Johnson 1980). Using ArcGIS version 10.1 (ESRI 2012 Redmond, California) and the Geospatial

Modeling Environment (GME © Spatial Ecology LLC), a population range was defined for each study wetland and consisted of a 100% Minimum Convex Polygon (100% MCP) that included all frog locations at that site, buffered by the maximum distance recorded between successive relocations for an individual frog at that site (Figure 3.1). Thus, each study wetland was assigned a unique buffer width in order to account for the movement patterns actually observed at each of the ponds and to quantify an appropriate area of available habitat for frogs tracked there (see Table 3.3 for buffer widths). As long-distance migratory movements were observed only at ravine wetlands and not upland wetlands, I avoided using a standard buffer size across all the study sites, as this method would create population ranges that overestimated available habitat at upland wetlands where frogs were largely constrained to wetland edges.

Since MCPs may not provide accurate estimates of habitat use at the home range scale for herptiles (Row & Blouin-Demers 2006), I defined home ranges for individual wood frogs using 95% kernel density estimates, where kernels were constructed for each tracked frog using a smoothing factor (h) that resulted in an area equaling that of a 100% MCP containing all recorded locations for that individual (Row & Blouin-Demers 2006; Edge et al. 2010) (Figure 3.2). As inadequate sampling can result in underestimates of home-range size (Girard et al. 2002), I also tested for a relationship between the size of an individual’s home range and the corresponding number of locations recorded for that frog using linear regression. Home range size was compared between the sexes and between frogs tracked at upland sites and frogs tracked at ravine sites using a univariate analysis of variance (ANOVA). Home ranges were log-transformed in order to meet assumptions of normality.

In order to quantify the availability of different habitat features, random points were generated throughout the population range and home ranges at each site. Within the buffered population range of each wetland, a series of random points was created based on the number of frog locations recorded for that site. Additionally, a separate set of random points was generated within the home ranges of each tracked frog. The number of random points generated within the home ranges was equal to the number of recorded locations for that individual. Only individuals with at least 10 relocations were used for the analysis (n = 30 frogs, 563 locations). As a result, habitat use information was determined for 10 of 11 study wetlands as, at one site (Pond 108), no frog was relocated 10 or more times.

I quantified and defined macrohabitat selection at both spatial scales (2nd- and 3rd-order) by using the distance-based approach (Conner and Plowman, 2001) following procedures outlined in Edge et al. (2010) and Paterson et al. (2012). For each point (random or used), the distance to the nearest representative of each of the nine land-cover categories was calculated using the Spatial Join tool in ArcGIS. At both spatial scales, the mean distance of use points (u_i) was compared to the mean distance for random points (r_i) for each cover category one level higher in the selection hierarchy. For 2nd order habitat selection, u_i values were calculated using the random points generated within each home range and r_i values were calculated using the random points within the population range. For

3^{rd}-order habitat selection, u_i values were calculated using the actual frog locations and r_i values were calculated using the random points within the home ranges. This process was repeated for each of the nine land-cover categories with individual frogs as the unit of replication. The average u_i values (representing use) were divided by the average r_i values (representing availability) to form a distance ratio ($d = u_i/r_i$) for each of the cover types and each frog. The ratio indicated whether frogs used locations closer to or farther from land-cover features than expected. The value of the vector ratio ($d = u_i/r_i$) would be 1 if frogs used available cover categories randomly. At both spatial scales (2^{nd} and 3^{rd} order), a vector of ratios measuring habitat selection was calculated for each of the radio-tracked frogs.

I used multivariate analysis of variance (MANOVA) to determine if the mean distance ratios for each land-cover category differed significantly from 1 (random use of land-cover features), using individual frogs as replicates. If land-cover categories were used non-randomly (significant result from MANOVA test), two-tailed t-tests with Bonferonni corrections for multiple tests were used to determine a rank of preference for each of the land-cover categories (Edge et al. 2010; Paterson et al. 2012).

To determine microhabitat selection, I compared the 13 measured microhabitat metrics at each use location to the same metrics at its paired random location. As I only measured microhabitat in 2012 and only at terrestrial locations, my sample size was substantially smaller (n = 181) compared to macrohabitat analysis (n = 563). As a result, analyzing microhabitat for individual frogs was not feasible and all locations were pooled. Use locations were compared to random locations with a Wilcoxon Signed Rank Test. All statistical analyses were conducted using SPSS (Version 10, IBM Corp. Armonk, NY, USA).

Results

Home Ranges

The average home range size for all tracked wood frogs was 1982.4 ± 130.0 m^2 (SE; range = 31.7 – 19 330.6 m^2). Home range size was not related to the number of relocations for tracked frogs (linear regression, $R^2 = 0.048$, $b = 32.02$, df = 28, $P = 0.246$). There was a significant effect of sex on home range size ($F_{[1,26]} = 4.741$, $P = 0.039$), with females having large home ranges than males. Neither wetland type (upland or ravine; $F_{[1,26]} = 0.036$, $P = 0.852$) nor the interaction between sex and wetland type ($F_{[1,26]} = 0.017$, $P = 0.898$) had a significant effect on home range size but frogs tended to have larger home ranges at upland wetlands than ravine wetlands (Table 3.4).

Land-cover Use and Composition

During the two field seasons of 2011 and 2012, a total of 563 unique frog locations were recorded for individuals with ≥ 10 relocations. Overall, 88.1% of frog locations occurred in water, grass / low shrub or tall shrub (Table 3.5). Some land-cover types (pavement and mowed grass) were almost completely avoided by tracked frogs; these categories accounted for < 1% of all relocations. In order to characterize the prevalence of the 9 land-cover categories across the 10 study wetlands, I assessed the landscape within 125 m of each wetland's edge (125 m represented the greatest distance travelled from a breeding pond by any tracked frog, see Chapter 2). On average, the most common land-cover type at the eight upland wetlands was lawn and garden followed by pavement and buildings. Tall shrub, bare ground and forest cover were relatively rare and accounted for the three lowest proportions of total area on the landscape (Table 3.6). All upland study wetlands had some representation of the nine cover types except for Pond 404, which had no forest cover within the 125 m buffer. Ravine wetlands were largely dominated by forest cover but also had modest amounts of grass / low shrub, open water and tall shrub cover (Table 3.6). Several land-cover categories were completely absent from 125 m buffers surrounding ravine wetlands (buildings, mowed grass and lawn/ garden).

Habitat Selection Analysis

Significant selection for habitat features was detected at both the 2nd- and 3rd-order scale. At the 2nd-order scale, average distances to habitat features for random points within the home ranges differed significantly from average distances to habitat features for random points within population ranges ($F_{[9,50]}$ = 74.063, P = 0.000). Figure 3.3 presents mean vector ratios for all nine land-cover types and indicates if habitat features were used more or less than expected according to availability (vector ratio (d) significantly different from 1.0). Water and grass/low shrub were the most preferred habitat features (lowest mean d values), followed by tall shrub, bare ground and mowed grass, respectively. Four cover categories showed a mean vector ratio greater than 1.0 (house/building, pavement, lawn/garden and forest), indicating that these habitat features were used less frequently than their availability on the landscape. Two of these land-cover categories (lawn/garden and buildings were significantly avoided by tracked wood frogs (*d* significantly greater than 1). Bonferonni-corrected pairwise comparisons indicated that water and grass/low shrub were equally preferred when compared to each other, but were significantly preferred over all other cover categories (Table 3.7). Tall shrubs were significantly preferred over building, pavement and lawn/garden but equally preferred relative to forest, mowed grass and bare ground.

At the 3rd-order scale, distances of wood frog locations to habitat features were significantly different than the distances of random points within the home range to these features ($F_{[9,50]} = 2.768$, $P = 0.013$). Again, water and grass/low shrub were the most preferred features followed by bare ground, all three of which had a mean distance ratio significantly less than 1.0 (Figure 3.4). All other land-cover types had distance ratios close to 1.0 and were used proportionally to their availability on the landscape. Bonferonni-corrected pairwise comparisons indicated that there were no significant differences in preference for the nine habitat types at the 3rd-order spatial scale (Table 3.8). Thus, although wood frogs selected three of the cover types more often than availability predicted, these cover types were not significantly preferred over the six others present on the landscape.

In addition to significant selection of macrohabitat features at both spatial scales, wood frogs also demonstrated significant habitat selection at the microhabitat scale (habitat features within 1 m^2 of locations). Frogs were located at sites with lower light levels, in closer proximity to water, and with greater coverage by shrubs and open water compared to random sites (Table 3.9). Frog locations were also characterized by significantly lower coverage by graminoids and herbaceous dicots than paired random sites. I did not detect a significant difference in percent cover of down woody debris, litter, moss and bare ground, or in soil moisture and plant height.

Discussion

Through radio-telemetry I was able to quantify habitat use over three spatial scales for wood frogs at urban wetlands of Edmonton, Alberta. Home range size for adult wood frogs varied drastically among individuals but did not differ significantly between upland and ravine wetlands. Wood frogs largely remained in and around their breeding ponds throughout the tracking period, selecting terrestrial habitat features in close proximity to water (un-mowed grass and shrubby cover) while avoiding human-modified land-cover (buildings and pavement). Contrary to my predictions, wood frogs did not significantly select for forest cover and generally avoided this cover type. At the microhabitat level, wood frogs selected for land-cover features that would likely reduce water loss (low light levels, close proximity to water and increased shrub cover).

Although several studies have quantified movement behaviour for wood frogs, only a few have determined adult home range sizes. In a simple mark-recapture study, Bellis (1965) observed average home range sizes of 64.5 m^2 (max = 368.3 m^2) at a Minnesota peat bog. Long et al. (2010) found that radio-tracked wood frogs in the boreal forests of Alberta had home ranges averaging 175 m^2

during the summer active period, and Blomquist and Hunter (2010) reported average spring (May – June) home range sizes of 285 m^2 for radio-tracked adults in Maine. Home range sizes observed for wood frogs at my study wetlands were significantly larger (mean = 1982.4 m^2; Table 3.4) than those listed above. However, direct comparisons between previously reported values and those documented by the present study should be done cautiously as methodology for determining home range size and tracking duration differed among studies. As Bellis (1965) relied solely on reencounters during foot searches to quantify wood frog home range size, recorded areas were likely grossly underestimated despite the extended duration of the sampling (July – September) and likely only represented minimum home range sizes. Both telemetry studies estimated home range size using 100% MCPs but were relatively short in duration (Long et al. – mean tracking period per frog = 20 days, Blomquist and Hunter – no mean tracking period reported but maximum was 36 days) compared to the present study (average tracking period = 43.8 days, maximum = 79 days). My results indicate that wood frogs at urban wetlands are capable of maintaining relatively large home ranges. It is possible that studies to date are underestimating the core areas used by this species and emphasis should be placed on extending the time over which individuals are tracked.

Wood frogs are considered a forest-dependent species, preferring closed-canopy, forested habitat to more open, grassland or shrubland habitat during upland terrestrial movements (Baldwin et al. 2006; Rittenhouse and Semlitsch 2009; Blomquist and Hunter 2010). As ravine sites contained significantly larger amounts of forest cover surrounding wetlands compared to upland sites (Table 3.6), I expected frogs tracked at these locations to have larger home ranges as, with a greater availability of suitable habitat, frogs would be able to travel farther distances from wetlands to find suitable summering grounds. However, long-distance movements away from breeding ponds were rare at ravine wetlands and I did not observe a significant difference in home range size between upland and ravine sites. In Chapter 2, I proposed that movement from ravine wetlands was relatively limited possibly due to the permanence of the waterbodies and risk of desiccation associated with terrestrial movements. With limited movement away from the ponds, behaviour of wood frogs at ravine wetlands closely resembled that observed for upland wood frogs, which could explain why we did not see significant differences in home range size between the two wetland types. Several upland wetlands also contained small islands upon which wood frogs were occasionally located (61/341 relocations at upland wetlands). These islands allowed wood frogs to expand their home ranges while avoiding certain predators (domestic cats) and remaining in close proximity to water.

Despite similarities in home range size between ravine and upland frogs, the overall size of population ranges (buffered areas that encompassed all home ranges for frogs tracked at a particular site) observed at the two wetland types differed significantly (Table 3.3) with ranges at ravine sites being significantly larger than ranges at upland sites. As ravine sites had a greater number of frogs tracked per site than upland sites, and also contained individuals that demonstrated migratory movements, it follows that population range size differed between the two wetland types.

Female wood frogs at my study sites had larger home ranges than males during the summer active-period. Because females employ different reproductive strategies and experience different energy costs associated with reproduction than males, female wood frogs will often travel farther from breeding ponds during the summer which could lead to larger home ranges compared to males (e.g., Regosin et al. (2003) in Massachusetts). Female amphibians will make significantly longer migrations than males following mating in order to find prime foraging areas where they can recoup energy lost in the production and laying of eggs, and accumulate enough energy for the formation of next spring’s eggs prior to hibernation. Males are better served by remaining close to breeding ponds during their summer active period and during hibernation to allow for an early arrival to breed in spring (Regosin et al. 2003; Rittenhouse and Semlitsch 2007b).

The presence of open water on the landscape proved to be an important habitat feature in explaining wood frog locations at all three spatial scales. Wood frogs selected microhabitat with greater cover of standing water than random plots and were also located significantly closer to open water than predicted based on its availability on the landscape. The selection of habitat closely associated with open water is likely driven by the need to maintain water balance during summer. As amphibian skin provides very little resistance to the movement of water (Jørgensen 1997), choosing habitat in close proximity to wetlands affords individuals the opportunity to replenish water lost to evaporation (Baldwin et al.

2006; Rittenhouse et al. 2008). Habitat located at the edge of wetlands and streams would also allow frogs to flee into aquatic habitat to avoid terrestrial-based predators like garter snakes (*Thamnophis spp.*) or humans (a perceived predator) (Bellis 1965). I observed significant selection for cattails (*Typha latifola* L.) at the microhabitat scale. Cattails are associated with damp soil conditions, are located in or close to standing water, and provide shade and litter at ground level, creating ideal microhabitat for wood frogs.

At my three ravine study sites, washouts and sandbars associated with oxbow ponds and adjacent streams were present and utilized by several tracked frogs. These areas were close to water (allowing for predator avoidance and osmoregulation) and were generally excellent sites for basking as they often contained little overstory vegetation. Due to sloughing and erosion, washouts often contained tunnels and hollows, within which I occasionally found tracked frogs. By seeking refuge in these cool, moist retreats, wood frogs would be able to avoid the risk of desiccation on hot days and remain concealed from predators (Seebacher and Alford 2002; Rittenhouse et al. 2008; 2009; Roznik and Johnson 2009). The 3rd-order scale habitat assessment indicated that frogs selected locations within their home range that were closer to bare ground habitat than predicted by availability. This could reflect the preference for these cool refugia on the banks of streams and ponds.

Wood frogs that did leave the protection of open water often remained within the grassy riparian zone surrounding wetlands. These riparian zones were dominated by un-mowed graminoids interspersed with shrubs (predominately willow and dogwood). Over 65% of all frog locations occurred in either grass / low shrub or tall shrub land-cover (Table 3.5); both cover types were associated with mean *d* ratios less than 1.0 at the 2nd and 3rd order spatial scales (grass / low shrub selected at both spatial scales, tall shrub selected at 2nd-order scale only). Selection for shrub cover was also significant at the microhabitat scale (Table 3.9). At both upland and ravine wetlands, tall grass and shrub cover was often the first upland vegetation present in the transition from the open water of wetlands to upland, terrestrial habitat.

Land-cover dominated by tall grasses and low shrubs provides opportunities for basking and thermoregulation (higher light levels than forested areas; mean light transmission at forest locations = 0.411 (proportion), mean light transmission at grass / low shrub locations = 0.721) while still providing shelter from predators and intense, direct sunlight (Heinen 1993; Constible et al. 2001; Walsh and Downie 2005). At the microhabitat scale, frogs selected habitat with significantly less grass and forb cover but greater proportions of shrubs than random plots (Table 3.9). Thus, within the grass / low shrub mosaic, frogs seem to prefer shrub cover over grassy cover, potentially due to the greater amount of litter and shade present under shrubs.

Tall shrubs especially offer appropriate habitat conditions for wood frogs at my study sites. Bartelt et al. (2004) and Browne (2010) both reported significant selection for shrub habitat by tracked western toads (*Anaxyrus boreas*) in Idaho and in Alberta, respectively. Not only does tall shrub cover provide litter and woody debris for shelter, the patchy canopy creates a mosaic of shaded and sunny sections at ground level, ideal for amphibian thermoregulation (Bartelt et al. 2004; Browne 2010). Finally, as areas with increased shrub cover often contain high invertebrate abundance and diversity (Ferguson 2001; Ferguson and Berube 2004), these areas likely provide excellent foraging opportunities for wood frogs.

Not surprisingly, wood frogs seemed to avoid human-modified land-cover (buildings, lawns and gardens, pavement). These cover types are associated with exposed, open areas that provide little in the way of shelter from desiccation or predation for amphibians (Mazerolle 2001; Mazerolle and Desrochers 2005; Ramirez et al. 2012). The radio-tracked individuals would occasionally cross mowed grass or pavement surfaces in order to reach more suitable land-cover; however, very few were actually relocated in these cover types (only nine of 563 recorded locations occurred in human-modified land-cover: seven in planting beds and gardens and two in mowed grass). As all relocations were made during daylight hours, it is unclear if these patterns would change during night when desiccation risks are reduced, potentially allowing frogs to exploit these more exposed areas. Future studies could focus on nocturnal habitat use of urban wood frogs to determine if selection for habitat features differs with time of day.

Contrary to my prediction, forest cover was not preferred by wood frogs and actually displayed the highest distance ratio value at the 2nd-order spatial scale (d = 1.43). As many previous studies have identified forest cover as essential habitat for migration and foraging, I expected wood frogs to show the greatest preference for closed-canopy forest (deMaynadier and Hunter 1999; Regosin et al. 2005). At upland wetlands, forest cover was relatively rare, accounting for a low proportion of the total land-cover (Table 3.6) and was often isolated from breeding ponds by distances greater than 30 m (see Chapter 2). Consequently, forest cover may have been too difficult to access for frogs at upland sites and habitats that existed closer to water were preferred (Grass/ Low Shrub and Tall Shrub habitat). Despite an abundance of forest cover present at ravine wetlands, few frog locations occurred in this land-cover type (18 / 222 locations at ravine wetlands). Although adult wood frogs select for forest cover during migratory movements in the spring and fall (Rittenhouse and Semlitsch 2007a; Baldwin et al. 2006), the importance of forest habitat during the remainder of the frogs' active season may be reduced. Most individuals tracked at ravine sites did not migrate and instead remained in close proximity to breeding ponds where open water was easily accessible for rehydration and dominant land-cover was grass or shrubs. As the ravine ponds had permanent hydroperiods, frogs were not forced to move away from breeding sites during the active season and may be less dependent on forest cover compared to wood frogs tracked in other systems.

Conclusions

Wood frogs at urban wetlands demonstrated significant habitat selection at all three spatial scales examined. Frogs selected sites closely associated with long grass and shrub cover, as well as water, at the macrohabitat scale and preferred shaded, shrubby habitat in close proximity to water at the microhabitat scale. They tended to avoid human-modified land-cover (lawns, gardens and pavement) and were less associated with forest habitat than previous studies would predict (deMaynadier and Hunter 1999; Regosin et al. 2005). Physiological constraints, both thermal and osmoregulatory, were likely key drivers in determining wood frog habitat use although isolation of breeding ponds, predation risk, and prey availability likely also played important roles.

My study describes how a representative anuran at urban wetlands uses terrestrial habitat surrounding breeding ponds and to my knowledge is the first study to quantify habitat use for an amphibian species in an urban environment at multiple spatial scales. These findings have direct applicability to urban planning and wetland conservation. Their potential for informing decisions on urban wetland management are discussed in Chapter 4.

Figures and Tables

Table 3.1 Classification of land-cover types used during the digitization of aerial photos of the landscape surrounding urban wetlands of Edmonton, Alberta.

Land-cover	Description
Pavement	Paved surface (road or sidewalk) often associated with high human and automobile traffic
Mowed Grass	City-maintained grass surface, mowed several times throughout the year
Lawn/ Garden	Mix of mowed grass and planted gardens (front and back yards associated with houses)
Building	House or other building
Water	Open water
Grass/Low Shrub	Un-mowed graminoids and low-lying shrubs
Forest	Land-cover dominated by tree species (either deciduous, coniferous or mixed-forest) with distinct canopy visible from air photos
Tall Shrub	Shrub cover (often *Salix spp.*) greater than 3.0 m in height
Bare Ground	Non-vegetated soil (e.g. sandy washout near stream, undeveloped residential lot or gravel walking paths)

Table 3.2 List of structural and abiotic variables used in the analysis of microhabitat selection by 30 wood frogs tracked at urban wetlands of Edmonton, Alberta in 2012.

Microhabitat variables in 1-m^2 plot *	**Description**
% Grass/Forbs	percent coverage by unmowed graminoids and dicots
% DWD	percent coverage by all downed woody debris
% Litter	percent coverage of ground by leaves or conifer needles
% Moss	percent coverage by bryophytes
% Bare Ground	percent coverage by unvegetated soil or pavement
% Shrub cover	percent coverage by all shrubs species
% Cattail	percent coverage by cattail
% Water	percent coverage by standing water
Soil moisture	% soil moisture collected from northeast corner of quadrat
Light transmission	plot light level (measured at centre) divided by ambient light level (proportion)
Distance to water	distance from centre of plot to closest standing water of any size
Mean grass/forbs height	mean height of non woody stems (heights taken from individuals closest to the four corners of the plot)
Mean shrub height	mean height of shrubs (heights taken from individuals closest to the four corners of the plot)

*although coverage by trees was assessed for each plot, the metric was removed from analysis due to infrequent occurrence (13 / 362 plots).

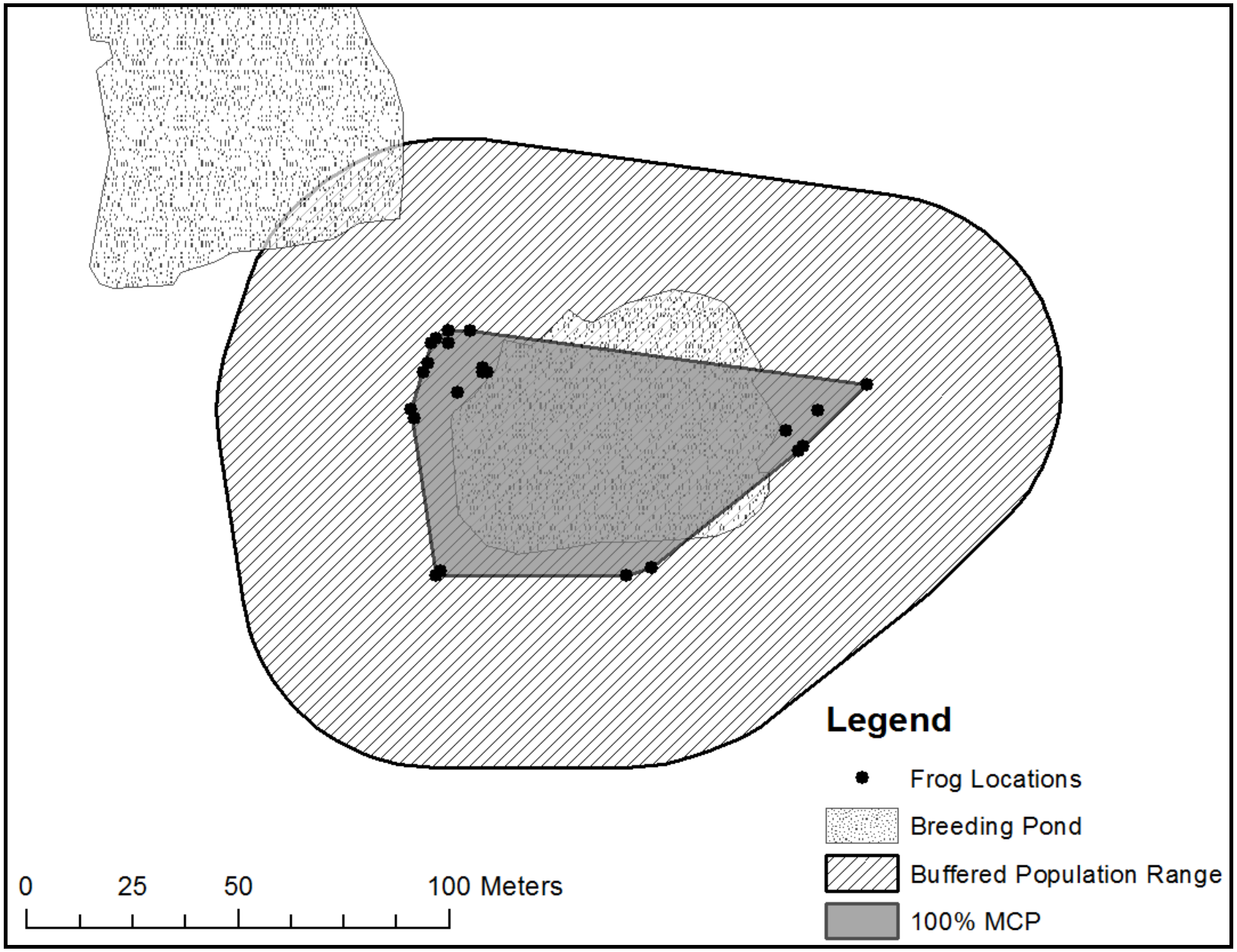

Figure 3.1 Sample 100% minimum convex polygon (100% MCP) enclosing all frog locations at Pond 109 with buffered population range. Frog locations represent all recorded points for the two wood frogs (Frog ID: 1091, 1092) tracked at Pond 109.

Table 3.3 Summary data for created polygons and buffers representing population ranges of wood frogs at 10 urban wetlands of Edmonton, Alberta. Area for 100% minimum convex polygons (100% MCP) surrounding all frog locations at each pond, the buffer distance applied to each 100% MCP and the resulting population ranges are listed.

Study Pond	Minimum Polygon Area (m^2)	Buffer Distance Applied (m)	Total Population Range (Polygon + Buffer) (m^2)
106	1841.0	70.8	34 163.3
109	4406.5	46.1	24 027.8
302	729.9	31.4	7 977.1
305	6461.0	118.0	92 192.1
308	4473.0	79.9	46 220.2
310	42685.0	129.1	197 076.6
314	23736.6	181.0	234 937.8
316	16594.8	174.0	204 285.9
404	16193.1	116.3	122 652.1
405	3463.5	74.3	39 673.6

* 10 of 11 study wetlands are presented as no frog from Pond 108 was included in habitat use analysis due to low rate of relocation at this site.

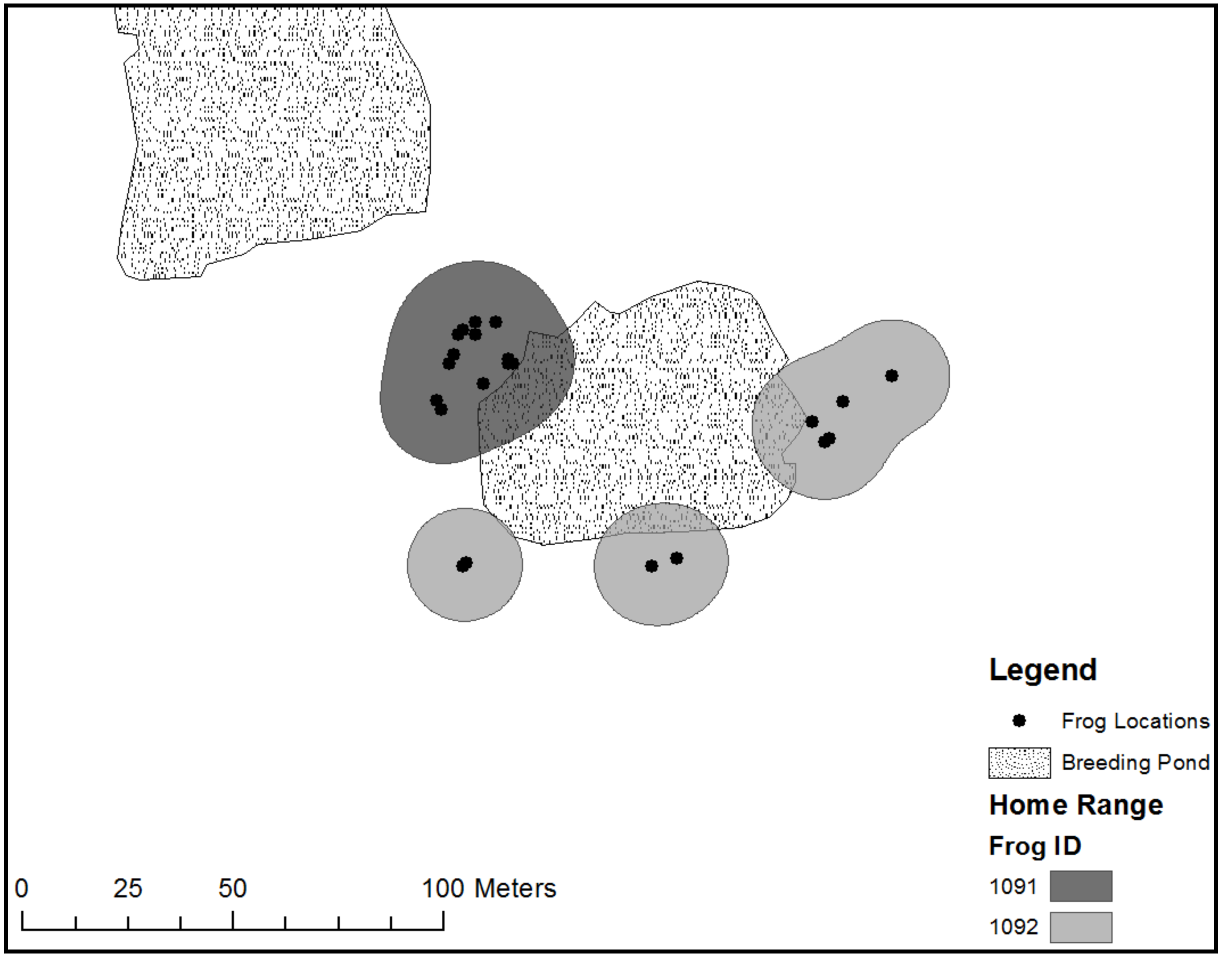

Figure 3.2 Home ranges for the two wood frogs (ID: 1091, 1092) tracked at Pond 109 created using 95% kernel density estimates.

Table 3.4 Mean and range (in square brackets) of home-range sizes for 30 wood frogs at 10 urban wetlands in Edmonton, Alberta. Values are stated as mean home range area (m^2) ± SE. Sample size of tracked frogs (n) for each group is provided in parentheses.

Sex	**Upland Sites**	**Ravine Sites**	**All Sites**
Male	457.0 ± 115.6 [57.8 – 1200.0] (10)	1932.4 ± 2765.1 [31.7 – 8991.6] (5)	948.8 ± 115.6 (15)
Female	2462.7 ± 914.2 [79.8 – 6195.9] (7)	3505.1 ± 2303.6 [81.3 – 19 330.6] (8)	3018.7 ± 1765.1 (15)
Both Sexes	1282.9 ± 440.9 (17)	2900.2 ± 1534.0 (13)	1983.7 ± 710.5 (30)

Table 3.5 Land-cover types used by wood frogs (n=30) at 10 urban wetlands in Edmonton, Alberta. The total number of relocations within each cover type are provided in parentheses (n).

	Upland		**Ravine**		**All Sites**	
	% Use	**(n)**	**% Use**	**(n)**	**% Use**	**(n)**
Bare Ground	0	(0)	6.8	(15)	2.7	(15)
Lawn / Garden	2.1	(7)	0	(0)	1.2	(7)
Water	13.8	(47)	31.5	(70)	20.8	(117)
Grass / Low Shrub	63.0	(215)	39.6	(88)	53.8	(303)
Mowed Grass	0.6	(2)	0	(0)	0.4	(2)
Tall Shrub	13.2	(45)	14.0	(31)	13.5	(76)
Forest	7.3	(25)	8.1	(18)	7.6	(43)
House	0	(0)	0	(0)	0	(0)
Pavement	0	(0)	0	(0)	0	(0)
Total	100	(341)	100	(222)	100	(563)

Table 3.6 Land-cover within 125 m buffers surrounding 10 urban wetlands of Edmonton, AB. Average values as well as minimum and maximum values for the percentage of total area of the nine land-cover types are summarized for upland wetlands (n = 7), ravine wetlands (n = 3) and all wetlands combined (n = 10).

Wetland Type	**Upland**			**Ravine**			**All Sites**		
	Mean ± SE	**Min**	**Max**	**Mean ± SE**	**Min**	**Max**	**Mean ± SE**	**Min**	**Max**
Pavement	19.5 ± 1.9	10.2	22.6	0.1 ± 0.1	0	0.3	13.7 ± 3.2	0	22.6
House	15.6 ± 1.6	8.5	19.9	0	0	0	11.0 ± 2.6	0	19.9
Lawn / Garden	22.2 ± 5.0	0.1	33.0	0	0	0	15.5 ± 4.5	0	33.0
Water	8.4 ± 1.4	3.6	14.0	6.8 ± 0.7	6.0	8.2	7.9 ± 1.0	3.6	14.0
Grass / Low Shrub	7.9 ± 3.0	2.4	21.1	9.3 ± 3.4	5.5	16.2	8.3 ± 2.0	2.4	21.1
Mowed Grass	15.2 ± 2.0	6.5	22.5	0	0	0	10.6 ± 2.7	0	22.5
Tall Shrub	1.2 ± 0.5	0.3	3.0	4.8 ± 0.1	2.7	6.2	2.3 ± 0.7	0.3	6.2
Bare Ground	2.1 ± 1.4	0.0	10.9	3.6 ± 0.3	3.0	4.1	2.5 ± 1.0	0	10.9
Forest	7.8 ± 4.7	0.0	27.8	75.2 ± 3.1	69.1	78.9	28.0 ± 10.7	0	78.9

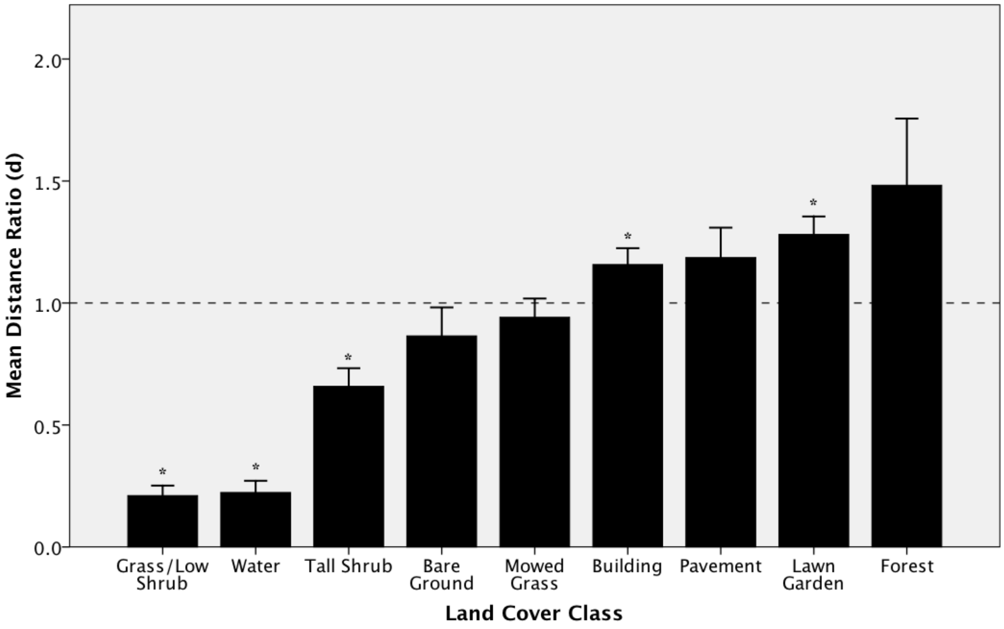

Figure 3.3 Mean distance ratios (*d* = u_i/r_i) + 1 SE for 2nd-order habitat selection (home range within population range) by wood frogs (n=30) tracked during 2011 and 2012 in Edmonton, Alberta. Ratios were calculated using a total of 563 random points. Cover categories are ranked most preferred (left) to least preferred (right) with an asterisk indicating where mean *d* values were significantly different from 1.0 (significant selection or avoidance).

Table 3.7 Mean distance ratios (*d*) and pairwise comparisons (two-tailed t-tests) for 2nd order habitat selection by 30 wood frogs at 10 urban wetlands in Edmonton, Alberta. Significant values ($P \leq 0.001$) are presented in bold and indicate where a particular cover type was significantly preferred over another.

Land-cover Class	**Mean Distance Ratio ($d=u_i/r_i$)**	Grass/ Low Shrub	Water	Tall Shrub	Bare Ground	Mowed Grass	Building	Pavement	Lawn / Garden
Grass/ Low Shrub	0.2107								
Water	0.2237	0.8366							
Tall Shrub	0.6585	**< 0.001**	**< 0.001**						
Bare Ground	0.8652	**< 0.001**	**< 0.001**	0.1398					
Mowed Grass	0.9413	**< 0.001**	**< 0.001**	0.0140	0.5885				
Building	1.1578	**< 0.001**	**< 0.001**	**< 0.001**	0.0335	0.0383			
Pavement	1.1864	**< 0.001**	**< 0.001**	**< 0.001**	0.0627	0.0959	0.8344		
Lawn/Garden	1.2813	**< 0.001**	**< 0.001**	**< 0.001**	0.0038	0.0023	0.2183	0.5095	
Forest	1.4362	**< 0.001**	**< 0.001**	0.0038	0.0411	0.0609	0.2185	0.3691	0.5503

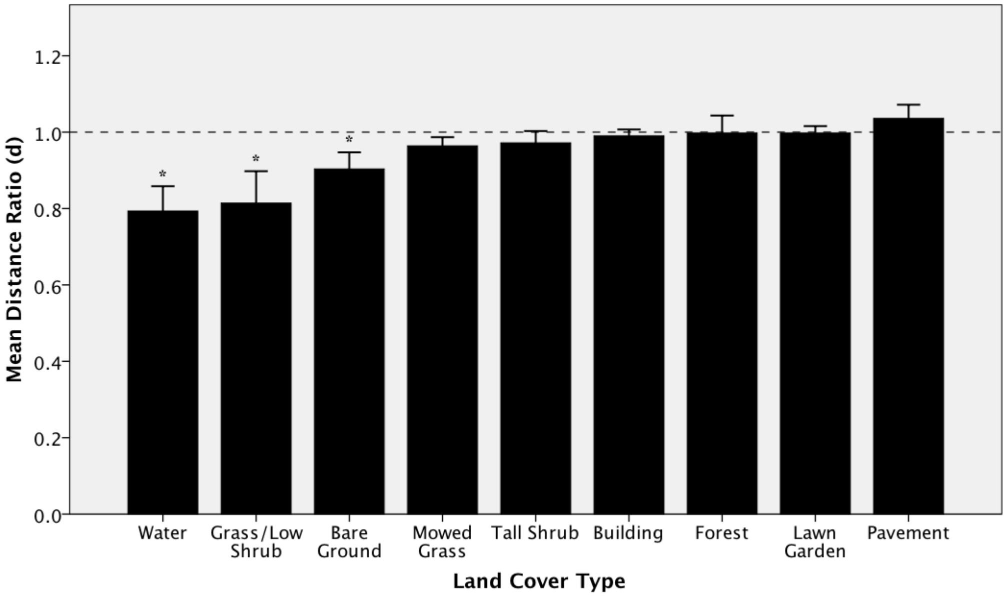

Figure 3.4 Mean distance ratios ($d = u_i/r_i$) + 1 SE for 3rd-order habitat selection (locations within home range) by wood frogs (n=30) tracked during 2011 and 2012 in Edmonton, Alberta. Ratios were calculated using a total of 563 random points. Cover types are ranked most preferred (left) to least preferred (right) with asterisks indicating where mean *d* values were significantly different from 1.0 (either selection or avoidance).

Table 3.8 Mean distance ratios (*d*) and *P* values from pairwise comparisons (two-tailed t-tests) for 3rd order habitat selection by 30 wood frogs at 10 urban wetlands in Edmonton, Alberta. Significant values ($P \leq 0.001$) are presented in bold and indicate where a particular cover type was significantly preferred over another.

Land-cover Class	**Mean Distance Ratio $(d=u_i/r_i)$**	Grass/ Low Shrub	Water	Tall Shrub	Bare Ground	Mowed Grass	Building	Pavement	Lawn / Garden
Grass/ Low Shrub	0.8145								
Water	0.7936	0.8439							
Tall Shrub	0.9719	0.0818	0.0161						
Bare Ground	0.9037	0.3459	0.1636	0.2061					
Mowed Grass	0.964	0.0886	0.0161	0.8398	0.2234				
Building	0.9902	0.043	0.0048	0.6042	0.0677	0.3592			
Pavement	1.0359	0.0018	0.0018	0.1823	0.0223	0.0967	0.2537		
Lawn/Garden	0.9978	0.0355	0.0036	0.4720	0.0497	0.2505	0.7585	0.3472	
Forest	0.9979	0.0528	0.0099	0.3071	0.1197	0.2367	0.8613	0.4884	0.9989

Table 3.9 Microhabitat structure and abiotic variables at random and wood frog locations (n = 181) at 10 urban wetlands of Edmonton, Alberta. Cover and abiotic variables are presented as mean values ± 1 SE and ranges along with P-values for Wilcoxon Signed Rank tests. Significant results from Wilcoxon tests are indicated with an asterisk (*).

Cover Type	**Random**	**Frog**	**Wilcoxon *P*-value**
Light Level (proportion of ambient)	0.69 ± 0.03 (0.01 - 1.0)	0.61 ± 0.02 (0.02 - 1.0)	0.006*
Distance to Water (m)	9.85 ± 0.75 (0.4 – 44.7)	8.91 ± 0.83 (0.02 – 44.5)	0.000*
Down Woody Debris (% cover)	5.12 ± 0.85 (0 – 80)	6.27 ± 0.90 (0 – 70)	0.114
Soil Moisture (%)	61.74 ± 2.29 (10 – 100)	61.77 ± 2.29 (10 – 98)	0.973
Litter (% cover)	21.8 ± 1.77 (0 - 89)	22.08 ± 1.59 (0 – 90)	0.945
Moss (% cover)	3.58 ± 0.99 (0 – 90)	2.94 ± 0.79 (0 – 96)	0.533
Grass/Forbs Cover (% cover)	53.94 ± 2.72 (0 – 100)	43.55 ± 2.24 (0 – 100)	0.000*
Grass/Forbs Height (cm)	20.45 ± 1.03 (3.3 – 89.8)	23.32 ± 1.09 (4.0 – 90.8)	0.112
Shrub Cover (% cover)	8.58 ± 1.13 (0 – 73)	12.42 ± 1.57 (0 – 90)	0.042*
Shrub Height (cm)	37.22 ± 6.30 (10.0 – 251.0)	44.45 ± 6.24 (8.0 – 300.0)	0.283
Water (% cover)	0.03 ± 0.03 (0 – 6)	4.12 ± 0.79 (0 – 55)	0.000*
Bare Ground (% cover)	8.16 ± 1.59 (0-100)	4.9 ± 0.95 (0-94)	0.477
Cattail (% cover)	1.30 ± 0.55 (0 – 80)	3.31 ± 0.76 (0 – 95)	0.000*

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Chapter 4. General Conclusions

Summary of Findings

Adult wood frogs tracked at urban wetlands of Edmonton, Alberta remained in close proximity to their breeding wetlands throughout the active season with few individuals travelling beyond 25 m of the margins of their ponds. Of the 50 individuals tracked over two summers, only five migrated from their breeding ponds to re-locate at nearby stream edges or small wetlands. All migrations occurred at ravine wetlands and were completed by large females. No migratory movements were documented at upland wetlands where frogs largely remained in grassy riparian zones fringing breeding ponds (average maximum distance travelled from upland breeding ponds = 14.1 m). Movement rates (DPD), average distances travelled from breeding ponds (DFBP) and maximum distances travelled from breeding ponds (MaxDFBP) did not differ significantly between upland and ravine sites or between males and females. However, on average, females and individuals tracked at ravine sites moved at faster rates and travelled greater distances from breeding ponds.

Wood frog movement was significantly correlated with short-term weather patterns. Frogs were located farther from water and demonstrated higher movement rates when temperatures and precipitation levels were higher. Periods of rain seemed to facilitate rare, long-distance movements from breeding ponds as all migratory movements occurred during or following heavy periods of rain. Frogs at upland sites were generally only located outside of wetland riparian zones when uplands were wet following precipitation.

I investigated the spatial scale at which land-cover had the greatest effect on movement from breeding ponds by tracked wood frogs. The land-cover models that I created could not accurately predict MaxDFBP (maximum distance travelled from breeding pond) or DFBP (average distance travelled from breeding pond), as even the best models, the pond type only model, explained little variation in the observed movements.

Wood frogs demonstrated significant habitat selection at all three spatial scales analyzed. At the 2nd-order spatial scale (selection of home range within population range), wood frogs selected home ranges closer to water, grass/ low shrub and tall shrub more often than predicted by availability. Buildings and lawns/ gardens were the only land-cover types that were significantly avoided by tracked individuals. Water and grass/ low shrub were preferred over all other cover types but were equally preferred when compared to each other. At the 3rd-order spatial scale (selection of locations within the home range), frogs were located significantly closer to water, bare ground and grass/ low shrub land-cover than predicted by availability. Although frogs selected habitat in close proximity to these three land-cover types, my results indicated that they were not significantly preferred over the other six land-cover categories present on the landscape. At the microhabitat scale, wood frog locations were characterized by lower light levels, higher cover by shrubs and open water and occurred closer to open water than random located plots.

Conclusions and Management Implications

Adult wood frog movement documented at urban wetlands of Edmonton differed substantially from patterns observed in other systems. I found that tracked frogs were largely confined to the edges and riparian zones of breeding ponds and movements away from these permanent bodies of water were rare and generally short. It is likely that the observed movement patterns reflect a complex suite of abiotic and biotic factors. Factors such as the density of breeding populations, weather conditions, the hydroperiod of breeding ponds, availability of summering grounds and the intervening land-cover between breeding ponds and summering grounds, all likely played a role in determining movement patterns at my 11 study wetlands. Movements at upland wetlands, where landscapes contained significant amounts of inhospitable land-cover and few accessible waterbodies, were especially constrained to the riparian zones surrounding breeding ponds.

Although rigorous estimates of population sizes were not conducted for my study, frogs encountered during perimeter foot searches and breeding effort observed in the spring (egg masses present), and during previous work at these wetlands (Scheffers 2010), indicated that adult population sizes at my upland study wetlands were small compared to other natural wetlands in the region (both ravine wetlands and upland wetlands in Miquelon Lake Provincial Park, see Chapter 2). The availability of appropriate habitat, providing shelter and food, surrounding breeding wetlands can have a significant effect on the size of amphibian populations (Rittenhouse and Semlitsch 2007b; Berven 2009). With limited suitable terrestrial habitat at several of my upland breeding ponds, adult wood frogs would be restricted in their ability to migrate from breeding ponds in order to escape density-dependent resource limitation. Low population sizes observed at these wetlands might reflect resource limitations, as the system would only be capable of supporting a limited number of breeding adults (Berven 2009). It is also possible that the sites are acting as sinks and the populations are either declining or are reliant on immigration of individuals from other wetlands in order to maintain a stable population size. The low number of sexually-mature adults present at these sites compared to ravine wetlands and other natural wetlands raises concerns over health of these populations as smaller populations of amphibians can lack genetic diversity, which increases their vulnerability to changes in environmental conditions and can increase risk of extinction due to stochastic events (Green 2003).

My study focused exclusively on the movement behaviour of adult wood frogs. Due to weight restrictions associated with the transmitter and belt package, I was unable to track movement or habitat use of smaller juveniles, including young of the year (YOY), via radio transmitters. However, movements and habitat use for juvenile wood frogs were documented using fluorescent powder during July and August of 2011 and 2012 (n = 19, mean weight: 5.41 g, SUL: 37.5). All movements by juvenile frogs were confined to the grassy riparian zones of wetlands, and frogs predominately selected habitat with tall grass, shrubs and cattail cover (unpublished data).

Juvenile wood frogs generally account for the majority of dispersal from breeding ponds (Marsh and Trenham 2001; Semlitsch 2000). These movements are unidirectional, probably only occur once in a lifetime, and generally involve travelling greater distances than those observed during adult migratory movements (Semlitsch 2008). It is unclear how human disturbance and land-cover would affect juvenile dispersal from my study wetlands. However, individuals attempting to leave upland breeding ponds would encounter the same barriers to movement (expansive areas of land with little protective cover) as migrating adults. As juvenile amphibians are more vulnerable to desiccation (high surface area to volume ratio), move at a slower rate and have lower stamina than adults (Beck and Congdon 2000; Smith and Green 2005), dispersal from most of my upland wetlands would likely involve significant physiological stress, potentially leading to high rates of mortality or failure to disperse. Despite apparent barriers to dispersal, recent work indicates that genetic differentiation, based on microsatellites, between breeding ponds in Edmonton (including 8 of my 11 study sites) is low (Furman B, unpublished data). These findings suggest that either gene flow is occurring among upland wetlands (presumably via dispersal of juveniles), or the time elapsing since the disturbance at these ponds and adjacent habitats has been too short (average age of upland wetlands = 11 years) to result in any meaningful genetic differentiation among breeding populations. Although the use of storm drains by dispersing amphibians has not been extensively studied, it is also possible that frogs from adjacent upland breeding ponds are capable of travelling through storm drains that connect upland ponds, establishing gene flow in a system where overland movements would be largely discouraged by inhospitable land-cover. Further research documenting dispersal from upland wetlands is needed to understand fully the isolation of these wood frog breeding populations.

Below, I provide suggestions for managing urban wetlands and their associated terrestrial habitats in order to improve habitat for amphibians and protect populations breeding at these sites (summarized in Table 4.1). I focus on improvements to upland wetlands as ravine sites are already largely protected from deleterious land-use changes and only modest levels of disturbance due to human activity exist at these sites (small walking paths, human visitors and domestic dogs (*Canus lupus familiaris*)). Although my recommendations pertain specifically to adult wood frogs, they can be applied to several other amphibian species (e.g., ambystomid salamanders and other ranid frogs) that share similar habitat requirements and terrestrial movement patterns as this widespread, pond-breeding species. As amphibian species often rely on similar habitats for both dispersal and migration (deMaynadier and Hunter 1999; Rothermel and Semlitsch 2002) my suggestions for land-cover management at urban wetlands also apply to the movement of multiple life stages (i.e. young of the year and older juveniles).

As many amphibian populations exist as metapopulations, they rely on a network of interconnected wetlands to promote the movement of individuals between breeding ponds and facilitate recolonization when local extinction has occurred at a particular site (Semlitsch and Bodie 1998; Skelly et al. 1999; Semlitsch 2000). Waterbodies that do not act as breeding sites (e.g., streams, very shallow temporary wetlands) can function as stepping-stones on the landscape for migrating or dispersing amphibians (Semlitsch 2000; Petranka and Holbrook 2006; Okonkwo 2011). Movement behaviour at my ravine wetlands and other studies also indicate that adult wood frogs will use stream edges or small temporary pools for summer foraging, loafing and even hibernation (Birchfield 2002; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a; Stevens et al. 2007).

The lack of accessible, alternative waterbodies on the landscape likely contributed to the limited movements from upland breeding sites. Petranka and Holbrook (2006) recommend creating and managing upland amphibian habitat as a complex of wetlands where multiple breeding ponds are interconnected by other small waterbodies of variable hydroperiod. Due to the extent of human disturbance in the tablelands of Edmonton and other large cities, the establishment of wetland complexes is likely unfeasible. However, installing streams or small ponds in close proximity to amphibian breeding sites could provide additional summering habitat for these animals while also encouraging migration and dispersal. Vegetation surrounding these water features and connecting them to breeding ponds should provide sufficient cover for amphibians to protect animals from the elements and predators.

Wood frogs at upland wetlands of Edmonton would likely benefit from higher coverage of shelter-providing habitat (e.g., taller grasses and shrubs) adjacent to breeding ponds. Grassy riparian zones surrounding upland wetlands were variable in size with buffers ranging in width from less than 5 m at some sites (Pond 106 and 302) to upwards of 35-40 m at others (Pond 108 and 109).

Frogs tracked at Ponds 108 and 109, where riparian zones were expansive, remained within 25 m of the water's edge during the tracking period. At pond 405, frogs were consistently located at distances between 25-30 m from water in shrubby habitat connecting the grassy riparian zone to forest cover.

As approximately 95% (447 of 463 upland relocations) of all wood frog locations occurred within 25 m of breeding wetlands, even at sites where protected vegetation extended beyond this point, maintaining buffers of this size surrounding all urban wetlands would likely provide important habitat for wood frogs breeding at these sites. Leaving larger patches of grass and low shrubs intact, especially in areas that connect forested land-cover with breeding ponds, would encourage migration movements from water and potentially allow frogs to locate higher-quality foraging patches at greater distances from wetlands.

Wood frogs were frequently located in stands of tall shrubs (predominately willow, *Salix spp.*) that bordered breeding pond edges, despite this cover-type accounting for a small proportion of the total cover surrounding ponds. By providing litter for shelter and variable light conditions at ground level, patches of shrubs act as important habitat for pond-breeding anurans (Constible et al. 2001; Bartelt et al. 2004 and Browne 2010). Planting or enhancing tall shrub cover within the 25 m buffers would provide important habitat for wood frogs and other amphibians at urban wetlands.

The shaded, closed-canopy environment of forest habitat facilitates terrestrial movement during migration and dispersal from breeding ponds (Rothermel and Semlitsch 2002; Regosin et al. 2005). Migrating wood frogs at ravine wetlands crossed through forest to reach summer foraging habitats and tracked individuals were occasionally located in forest stands, during short-distance movements away from their wetlands. In comparison, at upland sites, use of forest was extremely rare and occurred at only two of eight study sites. Chapters 2 and 3 describe how the configuration and abundance of forest stands at upland sites likely discouraged adult wood frogs from using this land-cover during terrestrial activity.

Relatively few frog locations occurred in forests compared to other cover types. Forest land-cover was used at only one upland wetland, Pond 405, where the relatively small (0.4 ha) patch of forest was located close to the breeding wetland (forest edge existed approximately 30 m from water). As preserving larger forest patches (several hectares) surrounding urban ponds is often not feasible (Windmiller et al. 2008), maintaining smaller forest patches (< 1.0 ha) within 50 m of breeding ponds could provide foraging areas and essential habitat for overwintering amphibians. Connecting breeding ponds to adjacent waterbodies (i.e., streams or other ponds) with forest patches in a stepping stone fashion should encourage adult migration and facilitate movements to summer foraging grounds (Semlitsch and Bodie 1998; Semlitsch 2000).

Small islands within ponds appeared to be important habitat features for wood frogs breeding at upland constructed wetlands as nearly 20% of all frog locations at these sites occurred on islands (61/341 locations). These islands were characterized by high proportions of tall shrub, unmowed grass and, at some sites, small forest patches and mats of moss. As access to these habitat features for humans and some terrestrial predators (house cats) is largely restricted, they provide areas for frogs to forage and bask. Creating islands during the construction of urban ponds could benefit amphibian populations whose movements are otherwise confined to the grassy riparian zones of breeding ponds.

My study provides an examination of post-breeding movement patterns and habitat use by anurans at urban wetlands and offers recommendations for improving habitat at breeding sites. Further research is needed to document the movement ecology and habitat use of other urban amphibian species, and different life stages. Future studies should focus on documenting dispersal for urban amphibians as this process is essential for maintaining gene flow between breeding populations, recolonizing ponds where local extinctions have occurred, and colonizing newly created ponds. Identifying landscape designs that facilitate both migration and dispersal from breeding ponds will be important for the persistence of amphibian populations in urban areas. As the expansion of cities is a prevalent phenomenon in today’s world, the replacement of natural wetlands and associated upland habitat with constructed ponds and urbanized land-cover is likely to continue. Land owners and managers need to be educated on the aquatic and terrestrial habitat requirements of amphibians residing in urban ponds in order to implement effective conservation and management strategies that promote wetland biodiversity and health.

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Table 4.1 Summary of recommendations for wood frog conservation in an urban setting. Recommendations are separated into those that pertain to construction and design of ponds and adjacent terrestrial habitat, and those that pertain to the management of existing urban breeding ponds.

Construction of Ponds	**Management of Ponds**
Include islands in the design of constructed wetlands. Plant islands with natural vegetation including grasses and tall shrubs.	Extend unmowed buffers surrounding breeding ponds to 25 m from water's edge.
Plant or protect natural stands of tall shrubs (e.g. willow) within 25 m of water's edge.	Create or enhance shrub cover (particularly tall shrub cover) within 25 m of pond margins
Retain patches of forest in close proximity to pond margins (< 50 m from pond) as overwintering and foraging habitat for frogs.	Create movement corridors between breeding ponds and forest patches and adjacent water bodies by planting overhead cover (trees, shrubs, tall grass).
Create a network of interconnected bodies of water as breeding sites providing access to additional ponds and streams for use by adults during the active season. Adjacent bodies of water should be constructed within 100 m (ideally within 50 m) to account for movement capabilities of adult and juvenile frogs.	
Connect breeding ponds and other bodies of water by retaining corridors of natural vegetation (natural patches of forest or unmowed grass) to encourage dispersal and migration.	

Appendix

Appendix A. Description of wetlands and counts of captured wood frogs (excluding young of the year and exceeding 25 mm in length) and radio-tracked individuals at 11 study ponds in Edmonton, Alberta during the period of May - August 2011 and 2012.

Pond	GPS Coordinates	Pond area (m^2)	Mean width of riparian zone (m)	Wood frogs captured in 2011 (# of individuals)	Wood frogs captured in 2012 (# of individuals)	Number of individuals radio tracked		Individuals tracked with ≥ 5 relocations	
						2011	2012	2011	2012
106	12U 341183 5926890	4538.0	4.7	18	20	2	4	1	2
108	12U 338354 5930391	27077.7	28.0	33	3	3	2	1	1
109	12U 338451 5930177	3777.3	23.3	1	10	0	4	0	2
302	12U 333204 5921875	4454.8	8.2	15	8	1	2	0	2
305	12U 331581 5922414	10491.8	6.2	15	7	6	2	5	1
308	12U 330193 5926481	10468.4	10.7	40	39	6	3	5	1
310	12U 330730 5925470	6111.0	8.2	62	38	7	3	4	2
314	12U 330901 5924264	3977.9	10.8	21	35	3	4	3	3
316	12U 330265 5928318	4031.6	11.1	26	27	8	5	2	4
404	12U 322520 5930589	23092.9	15.7	13	15	4	3	3	3
405	12U 322777 5931212	26964.1	14.9	44	50	3	5	1	4

Appendix B. Number of adult male (M) and female (F) wood frogs radio-tracked at the two wetland types (upland and ravine).

	2011		2012		
	M	**F**	**M**	**F**	**Total**
Ravine Wetlands	1	8	7	3	**19**
Upland Wetlands	6	10	11	4	**31**
Total	**7**	**18**	**18**	**7**	**50**

Appendix C. Summary of three movement parameters; mean distance from breeding pond (DFBP), mean maximum distance from breeding pond (MaxDFBP) and mean distance traveled per day (DPD) for 50 wood frogs (25 males, 25 females) tracked during the active period of 2011 and 2012 in Edmonton, Alberta.

	All Upland Wetland Frogs	**All Ravine Wetland Frogs**	**All Males**	**All Females**	**All 2011 Frogs**	**All 2012 Frogs**
Mean ± SE DFBP (m)	5.7 ± 1.4	17.7 ± 6.9	6.9 ± 1.8	13.7 ± 5.4	12.0 ± 5.4	8.6 ± 1.9
Mean ± SE MaxDFBP (m)	14.1 ± 2.3	32.4 ± 10.2	13.9 ± 2.8	28.2 ± 7.9	23.2 ± 7.9	19.0 ± 3.3
Mean± SE DPD (m/day)	5.2 ± 0.5	7.6 ± 1.6	5.9 ± 0.7	7.2 ± 1.1	6.6 ± 1.0	6.5 ± 0.9

Appendix D. Summarized percent land-cover for all buffers surrounding 11 urban wetlands of Edmonton, AB. Mean values ± SE for percentage of total area of nine land-cover types are summarized for upland wetlands (n = 8), ravine wetlands (n = 3).

	Ravine Wetlands				
Buffer Size	**10m**	**25m**	**50m**	**100m**	**125m**
Bare Ground	1.1 ± 0.6	1.2 ± 0.4	1.5 ± 0.3	1.4 ± 0.1	1.8 ± 0.1
Pavement	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1
Building	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Lawn/ Garden	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Water	0.2 ± 0.2	0.6 ± 0.0	1.9 ± 0.1	2.6 ± 0.5	2.9 ± 0.1
Grass/ Low Shrub	28.4 ± 7.8	16.7 ± 0.6	12.2 ± 3.4	10.1 ± 3.9	9.6 ± 3.5
Mowed Grass	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Tall Shrub	7.5 ± 3.6	9.6 ± 2.1	8.9 ± 0.7	5.2 ± 0.8	5.0 ± 1.1
Forest	62.6 ± 7.6	70.5 ± 2.0	73.9 ± 4.4	78. ± 5.0	77.6 ± 3.3
	Upland Wetlands				
Buffer Size	**10m**	**25m**	**50m**	**100m**	**125m**
Bare Ground	1.3 ± 0.5	1.1 ± 0.3	1.7 ± 0.6	2.6 ± 1.5	3.0 ± 1.9
Pavement	3.6 ± 1.5	5.9 ± 1.5	10.8 ± 2.2	19.4 ± 3.0	18.9 ± 2.8
Building	0 ± 0	1.0 ± 0.5	10.7 ± 2.5	14.2 ± 2.6	15.0 ± 2.5
Lawn/ Garden	3.8 ± 2.0	7.9 ± 2.8	9.1 ± 2.6	9.5 ± 2.4	9.8 ± 2.3
Water	0.3 ± 0.2	0.2 ± 0.1	0.5 ± 0.3	1.6 ± 0.9	1.5 ± 0.9
Grass/ Low Shrub	54.6 ± 7.6	32.1 ± 6.7	18.3 ± 4.4	10.5 ± 2.9	9.6 ± 2.8
Mowed Grass	14.1 ± 5.7	23.2 ± 7.8	18.8 ± 5.1	14.8 ± 3.0	14.0 ± 2.7
Tall Shrub	12.7 ± 3.0	7.0 ± 2.0	3.4 ± 1.0	1.7 ± 0.6	1.4 ± 0.5
Forest	6.3 ± 6.3	9.4 ± 7.4	14.0 ± 6.9	12.0 ± 5.4	11.1 ± 4.6