Canadian Journal of Zoology
Revue canadienne de zoologie

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Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2016-0298.R2
Manuscript Type:	Article
Date Submitted by the Author:	08-Aug-2017
Complete List of Authors:	Taylor, Murdoch; University of Alberta Paszkowski, C.A.; Department of Biological Sciences
Keyword:	habitat use, movement behaviour, urban wetlands, <i>Lithobates sylvaticus</i> , wood frog, wetland management, urbanization

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Draft

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Abstract

Habitat loss and degradation linked to urbanization threaten amphibian populations globally, yet studies examining amphibian behaviour and habitat use in cities are rare. Through the use of radio telemetry, we examined the postbreeding (May – October) movement behaviour and habitat use of adult wood frogs (*Lithobates sylvaticus* LeConte, 1825) at natural and constructed urban wetlands in Edmonton, Alberta, located in the semi-arid, aspen parkland of Canada. Movement from breeding wetlands was limited, with most tracked individuals remaining within 25 m of ponds in grassy riparian areas. Long-distance migratory movements were rare and only occurred at natural sites with relatively high proportions of forested land surrounding wetlands. In general, tracked frogs showed a preference for habitat close to water that provided shelter from desiccation and predation (e.g., unmowed grass and stands of shrubs). Our findings have implications for the management of wetlands and conservation of amphibian populations in urban environments.

Key Words: habitat use, *Lithobates sylvaticus*, movement behaviour, urban wetlands, urbanization, wetland management, wood frog

Introduction

Globally, the human population living in urban areas has nearly quadrupled since 1950 (UNHSA 2011). 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). Widespread declines of amphibians have been well documented over the past several decades and 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).

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 many types of land-cover 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 substantially different from that observed in pristine, “natural” systems. Understanding how urbanization affects habitat use and behaviour will lead to more effective management strategies for protecting amphibians in these environments (Cushman 2006; Birchfield and Deters 2005; Ramirez et al. 2012).

The wood frog (*Lithobates sylvaticus* LeConte, 1825) is a pond-breeding amphibian found throughout a large proportion of North America. In recent years, it has been used as a model species for documenting the effects of land use changes on amphibian populations (Cline and Hunter 2014; Coster et al. 2015; Earl and Semlitsch 2015; Veysey Powell and Babbitt 2015). After mating in the spring, adults leave breeding ponds and enter the surrounding terrestrial environment. Migratory movements from breeding ponds are often triggered by warm temperatures and periods of precipitation (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007b; Semlitsch 2008). Studies of movement behaviour conducted in Maine, South Carolina, and Missouri found that wood frogs typically travel towards moist, wooded habitats or stream edges, often selecting forest cover for migratory movements (deMaynadier and Hunter 1999; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a; Pitt et al. 2017). 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 for populations in Maine. During terrestrial activity, frogs tend to select shaded habitat (often closed-canopy forest) characterized by moist ground cover and downed woody debris (Constible et al. 2001; Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a; Otto et al. 2013).

Our current knowledge of wood frog movement behaviour and habitat use is derived primarily from studies conducted in undisturbed habitat or habitat altered by forestry or agriculture practices. The majority of previous studies took place in vernal pond systems of Maine and Missouri, USA. Comparatively little is known about the post-breeding activity of wood frogs in the northern and western portions of its range, or in urban settings, which is true, as noted, of most amphibian species globally (but see Husté et al. 2006; Montith and Paton 2006; Ramirez

et al. 2012; Garnham et al. 2015). Given the fact that the wood frog has the largest range of any amphibian in North America, and that in Alberta, Canada, where our study took place, it occurs in eight of 10 recognized ecoregions (Russell and Bauer 2000), we expected wood frogs to prove adaptable in their behavior and habitat-use patterns.

We used radio telemetry to i) quantify movement rates and distances travelled from breeding ponds by adult wood frogs and ii) document macrohabitat and microhabitat use at wetlands within the city of Edmonton, Alberta, Canada. We predicted that wood frog migratory movements and habitat use in the drier and urbanized environment of Edmonton would differ from patterns documented for populations from forested areas in the northeastern and central United States. We predicted that wood frogs would move shorter distances from their breeding ponds compared to movements observed in other portions of their range due to the limited availability of nearby areas offering moist terrestrial habitat for use during the active foraging season, as well as the requirement of travel from breeding ponds through dry, inhospitable habitat to reach moist terrestrial sites. We also predicted that wood frog behavior would differ between populations living on natural and constructed upland ponds in residential and industrial areas within Edmonton versus populations living on natural ravine wetlands within city parks, as the extent of inhospitable habitat (including lawns, buildings, and roads) around upland ponds is much greater (Scheffers and Paszkowski 2013). To our knowledge, this study is the first assessment of amphibian habitat use at multiple spatial scales in an urban environment for a species that is often characterized as a “forested-habitat obligate” and whose local decline or absence is cited as an indicator of forest fragmentation and destruction (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a). As the loss and degradation of natural habitat in association

with urbanization remains a pervasive threat to amphibians, increased understanding of how these animals successfully persist in such settings could guide the future design and protection of urban wetlands and associated terrestrial habitat. As noted in a recent review by Aronson et al. (2017), cities have the potential to become preserves for biodiversity on a global scale through the management and planning of urban green spaces, which were the focus of our study in Edmonton.

Materials and Methods

Study Sites

Adult wood frogs were selected for radio-tracking from 11 wetlands in north-central Alberta, Canada within the city of Edmonton, which is located in the aspen parkland ecoregion, a transitional zone between the mixed-grass prairie to the south and the mixed-wood boreal forest to the north (see Scheffers and Paszkowski (2013) for further descriptions of study sites). Wood frog breeding and juvenile recruitment have been recorded at urban wetlands throughout the city (Scheffers 2010). Populations have apparently persisted in natural, ravine wetlands for over 100 years and likely 20-30 years in the older constructed wetlands. Our research suggests that populations at individual ponds are not genetically isolated and have not suffered genetic bottlenecks (Furman et al. 2016). Immediately prior to development, upland sites were used for agriculture.

Daily 24 h average temperatures during the wood frog active period (May to October) in Edmonton are 13.9 °C (average daily minimum temperatures = 7.4 °C) and the average monthly precipitation total during this period is 57.4 mm, reflecting a semi-arid climate (Environment

Canada 2016). Of the 11 study wetlands, seven were constructed stormwater ponds located in upland residential and industrial developments. The terrestrial habitat surrounding these wetlands generally consisted of a narrow band of taller riparian vegetation (mean width = 13.3 m) encircled by a mosaic of altered habitat (mowed grass, houses, pavement, etc.) and patches of aspen-dominated forest (Fig. 1). Riparian vegetation included grasses, sedges, shrubs (*Salix spp.*, *Rosa acicularis* Lindl, 1820 and *Cornus sericea* L., 1753) and scattered trees (*Populus tremuloides* Michx., 1803, *Populus balsamifera* L., 1753, *Betula papyrifera* Marsh., 1785, and *Picea mariana* Miller, 1888). In addition to the seven constructed upland sites, frogs were tracked at one natural upland site that served as a stormwater drainage pond. The riparian zone of this remnant natural pond closely resembled that of the seven constructed wetlands in vegetation composition and width. For additional descriptions of the limnology and morphometry of the wetlands themselves, see Scheffers and Paszkowski (2013).

Frogs were also tracked at three natural, oxbow wetlands located in Whitemud Creek ravine. The ravine is part of Edmonton's 7,400 ha North Saskatchewan River Valley park system (https://www.edmonton.ca/activities_parks_recreation/parks_rivervalley/river-valley-parks.aspx). The vegetation structure surrounding the ravine wetlands consisted of a narrow, open riparian zone (< 10 m wide) that transitioned quickly into forested slopes dominated by *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera*, *Picea mariana* and *Picea glauca* Voss, 1908 (Fig. 2). The mean pairwise distance between all study wetlands was 8.3 ± 0.6 km (SE) (Range: 0.1 – 18.9 km).

We digitized colour satellite images (map scale = 1:5000) taken in 2011 with 50-cm resolution (Source: DMTI Spatial) using ArcGIS 10.1 software package (ESRI, Redlands, USA) for all

study wetlands and created a map documenting the occurrence of nine land-cover categories (Table 1). Polygons for each land-cover category were created for an area within a 500 m buffer surrounding each study wetland.

Data Collection

Wood frogs were captured for tracking during foot searches in spring, predominately during May, and opportunistically throughout the summer in 2011 and 2012¹. Frogs encountered and captured after the end of May, which marked the end of breeding, were all located on the margins of study wetlands; all tracked frogs were initially captured at locations < 10 m from study wetlands. Each captured frog was weighed, sexed and measured for snout-urostyle length (SUL). The frog's sex was assigned by the presence of nuptial pads for males, and by colour and size (Russel and Bauer 2000). Following measurements, adults weighing > 8.0 g were retained for radio-tracking. We used BD-2N radio transmitters (0.4 g) with a battery life of approximately 30 days (Holohil Systems Ltd., Carp, Canada). Transmitters were attached using external waist belts composed of silicone tubing (outside diameter = 2.2 mm). The combined mass of transmitters plus belt was always less than 10% of the frog's mass and typically less than 7% (average mass of tracked individuals = 11.92 g) (Richards et al. 1994; Indermaur et al. 2008). All work was carried out under an approved University of Alberta Animal Use and Care Committee protocol (AUP00000043) and a wildlife research and collection permit issued by Alberta Environment and Sustainable Resource Development.

Frogs bearing transmitters were released within 5 m of their original capture sites and relocated during daylight hours every 2-3 days (average = 2.2 days) using a Lotek Biotracker receiver

¹ See Table S1 for list of tracked wood frogs and their respective tracking periods.

(Lotek Wireless Ltd., Newmarket, Canada) with three-element Yagi antenna. Individuals were tracked from May to October in 2011 and from May to September in 2012. For each frog relocation, we recorded the individual's positional coordinates using either a Garmin© GPSMAP 62s handheld unit (Garmin Ltd., Canton of Schaffhausen, Switzerland) or a Trimble GeoExplorer 3000 series (Trimble Navigation, Ltd., Sunnyvale, USA), and classified the macrohabitat as one of the nine land-cover categories (Table 1). Field staff made every effort to avoid disturbing tracked individuals when locating frogs. If the transmitter signal did change in strength or direction during the relocation process, indicating movement, the location where the frog was first detected was used for spatial analysis. Measurements of the straight-line distance to the study wetland where the frog was originally released (measured to closest shoreline; locations in the water were assigned a distance of 0 m), as well as distance from previous location, were also calculated at this time.

In 2012, we collected microhabitat information from a 1.0 m² quadrat centred on each frog's location. Only terrestrial relocations at least 1.0 m from the previous location record were assessed for microhabitat information. At each frog location, we visually estimated the percentage of the quadrat occupied by several cover-type categories (e.g., graminoid plant, leaf litter, shrub), quantified abiotic parameters (e.g., soil moisture, light levels), measured average height of vegetation, and recorded distance to closest standing water (see Table 2 for full list of microhabitat measurements). Light levels were measured using a handheld light meter (General Electric, Type 217). To document microhabitat availability, each frog-location plot was paired with a random plot of equal size in which the same microhabitat parameters were measured. Random plots were placed 5.0 m from the frog's location point in a randomly-selected compass

bearing oriented towards terrestrial land cover. We chose a distance of 5.0 m based on the mean distance travelled per day by frogs tracked in 2011.

Movement Analysis

Of the 80 adult wood frogs tracked in 2011 and 2012, only those individuals with five or more relocations were included in analyses ($n = 49$). For each tracked individual, three parameters were used to quantify movement patterns in terrestrial environments: mean distance travelled from study wetland (DFW), maximum distance travelled from study wetland (MaxDFW), and mean distance per day (DPD) travelled. DFW and MaxDFW were both calculated based on the straight-line distance from each frog's locations to the edge of the study wetland where it was released. DFW serves as a measure of the distance travelled from study wetlands averaged across all observed locations and MaxDFW represents the greatest straight-line distance each frog was relocated from its study wetland's edge during the entire tracking period.

A simple two-sample t-test was performed to determine if tracking duration was significantly different between female and male frogs. A series of general linear models (GLM) was used to determine the effect of sex, tracking year, frog size (SUL), and study wetland type (i.e., upland or ravine) on the three movement parameters. We included number of relocations recorded for each frog as a covariate in each GLM to account for the disparity in length of tracking period among individuals. All three response variables (i.e., the movement parameters) were log-transformed to meet assumptions of normality and homogeneity of variance.

Habitat Use Analysis

Johnson (1980) proposed that wildlife will select habitat in a hierarchical nature and that 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). We adapted Johnson's (1980) habitat selection hierarchy to define wood frog macrohabitat use at two spatial scales: 2nd order (selection of home range within the population range) and 3rd order (selection of locations within home range). We also characterized microhabitat of our radio-tracked frogs (described above). Using ArcGIS, the range of the wood frog population was defined for each study wetland. This consisted of a 100% Minimum Convex Polygon (100% MCP) that included all frog locations at that site recorded during both tracking years (average number of locations per site = 59.6 ± 6.8 [se]), buffered by the maximum distance recorded between successive relocations for tracked frogs at that site (Fig. 3). Thus, each study wetland was assigned a unique buffer width based on the maximum distance any tracked frog traveled from that wetland.

Home range was mapped for 30 individual tracked frogs to delineate a second spatial scale (3rd order) at which habitat use could be assessed, in addition to the population ranges described above. For the purposes of this study, we use the term "home range" to describe the area encompassing all of an individual tracked frog's locations recorded during the active season. As most radio tracked frogs were not tracked for the entirety of the study populations' known active season (May to October), our calculation of home range likely does not capture the entire area that individual frogs utilized annually, but offers a workable approximation.

Because MCPs may not provide accurate estimates of habitat use at the home-range scale for herptiles (Row and Blouin-Demers 2006), home ranges for individual wood frogs were generated using 95% kernel density estimates. 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 and Blouin-Demers 2006; Edge et al. 2010). All kernel density estimates were created in R (R Foundation for Statistical Computing, Vienna, Austria) using the *adehabitatHR* package (v. 0.4.14). Inadequate sampling can result in underestimates of home-range size (Girard et al. 2002); studies based on radio-tracked animals indicate that estimated range area increases with the number of recorded locations, following a logistical curve that eventually plateaus at the true home-range size (Alberts 1993; Girard et al. 2002). Therefore, we examined the relationship between the size of an individual's home range and the total number of locations recorded for that frog. Although the pattern observed for our radio-tracked frogs deviated from a logistic relationship, home-range sizes initially plateaued at 10 relocations. Regression analysis confirmed that the number of relocations did not significantly affect home-range size for frogs with at least 10 locations ($R^2 = 0.109$, $P = 0.08$). We therefore only included individuals with at least 10 relocations in habitat-use analysis ($n = 30$, 596 locations).

To quantify the availability of habitat features, random points were generated throughout the population range and individual home ranges at each site. Within the buffered population range of each wetland, a series of random points was created; the number of points was equal to the number of frog locations recorded for all tracked frogs at that study wetland. A separate set of random points was also generated within the home ranges of each tracked frog with the number of random points generated equal to the number of recorded locations for that individual. We quantified macrohabitat selection at both spatial scales (2nd- and 3rd-order) by using the distance-based approach (Conner and Plowman 2001). 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 from one level higher in the selection hierarchy. Thus 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 3rd-order habitat selection, u_i values were calculated using the actual frog locations and r_i values were calculated using the random points within that frog's home range. 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 categories and each frog. A vector of ratios measuring habitat selection was calculated for each of the radio-tracked frogs for both the 2nd and 3rd order spatial scales.

We used multivariate analysis of variance (MANOVA) to determine if the mean distance ratios for each land-cover category differed significantly from 1.0 (random use of land-cover features), using individual frogs as replicates. If land-cover categories were used non-randomly (i.e., result of MANOVA test was significant), 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, we compared the 13 measured microhabitat metrics at each use location to the same metrics at its paired random location. As microhabitat features were only measured in 2012 and only at terrestrial locations, sample sizes were smaller ($n = 181$) compared to macrohabitat analysis ($n = 596$). As a result, analyzing microhabitat for individual

frogs was not feasible and all locations were pooled. Although pooling locations is not ideal (because of auto-correlation between each individual's sequential locations), our sampling schedule that recorded frogs' locations every 2-3 days, allowed individuals sufficient time to select different microhabitats between location fixes. We also excluded from microhabitat analysis any relocations that occurred within 1.0 m of the individual's previous location. Because microhabitat data were not normally distributed and transformations were ineffective, we used Wilcoxon signed rank tests to compare characteristics of locations used by frogs to those of random locations. All statistical analyses were conducted using SPSS Ver. 20 (IBM Armonk, NJ, USA) or R.

Results

Tracking Frogs and Movement Patterns

A total of 49 radio-tracked wood frogs generated at least five locations: 25 frogs in 2011 and 24 in 2012. In total, 24 males and 25 females were tracked across the 2 years; 18 frogs were tracked at the three natural ravine sites compared to 31 tracked at eight upland sites. On average, individuals were radio-tracked for 33.2 ± 3.0 days (mean $\pm$ SE) resulting in a total of 724 locations. Females were monitored for longer periods (mean = 36.4 ± 4.6 days) than males (mean = 29.9 ± 3.7 days) and radio-tracked females (mean SUL = 49.4 ± 0.7 mm; mean weight = 13.5 ± 0.7 g) tended to be larger than males (mean SUL = 44.5 ± 0.7 mm, mean mass = 10.2 ± 0.5 g; Taylor 2014).

Most frogs remained within the riparian zones of wetlands during the active season and only occasionally used adjacent upland habitat, often during periods of increased precipitation, then returned to the wetland margins (mean DFW = 9.9 ± 2.5 m SE; mean MaxDFW = 20.0 ± 3.0 m).

Approximately 70% ($n = 513$) of the 724 locations recorded occurred within 5.0 m of the edge of the study wetlands.

Of the 49 frogs tracked over the two-year period, six individuals (four in 2011 and two in 2012) made longer, one-way trips away from their study wetlands, re-locating to terrestrial habitat adjacent to streams or small pools of standing water. We classified these individuals as “migrants” (Semlitsch 2008), as they never returned to their respective study wetlands during the tracking period and distances travelled were relatively large (average MaxDFW = 31.4 m) compared to the temporary movements away from study wetlands observed for the majority of tracked frogs. All migrants inhabited ravine wetlands where they presumably bred before travelling through terrestrial habitat (typically forest) to reach their final summer destinations. Three of five individuals made migrations from study wetlands during late May or early June and the remaining two during late July and early August. Recorded migration movements occurred during or immediately following rain.

Movement Parameters

Of the five explanatory variables included in linear models explaining wood frog movement parameters, only sex had a statistically significant effect. Movement rates (DPD) for females (mean DPD = 7.9 ± 1.1 m/day) were significantly higher ($\beta = -0.232$, $P = 0.033$) than for males (mean DPD = 5.3 ± 0.6 m/day) (Fig. 4). Although not significant at an α -level of 0.05 ($\beta = -0.491$, $P = 0.052$), on average, females (mean DFW = 12.7 ± 4.6 m) were also located farther from the study wetlands than males (mean DFW = 6.9 ± 1.7 m). Similarly, maximum distances travelled from study wetlands were significantly greater ($\beta = -0.519$, $P = 0.047$) for female frogs (mean MaxDFW = 24.7 ± 5.1 m) compared to males (mean MaxDFW = 15.1 ± 3.0 m) (Fig. 4).

The number of relocations for radio-tracked frogs did not significantly affect DPD ($\beta = -0.001$, $P = 0.828$), DFW ($\beta = 0.008$, $P = 0.496$), or MaxDFW ($\beta = 0.018$, $P = 0.117$) and we detected no significant effect of tracking year, wetland type, or frog size on the three movement parameters.

Home ranges

The average home-range size for the 30 wood frogs included in habitat-use analysis was $2259.6 \pm 740.8 \text{ m}^2$ (range = $74.3 - 20\,832.4 \text{ m}^2$). In general, home ranges were narrow, and often confined to the margins of breeding wetlands. Relocations suggested that tracked individuals typically travelled along shorelines but also occasionally swam across ponds to the opposite side.

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 ($F_{[9,50]} = 32.27$, $P < 0.001$; Table 3). Table 3 presents mean distance ratios for all nine land-cover types and indicates if habitat features were used more or less than expected based on availability (distance ratio (d) significantly different from 1.0). Water, grass/low shrub, and tall shrub all had mean distance ratios significantly lower than 1.0, indicating selection for these cover types by wood frogs at the broadest, 2nd-order scale. House/building, pavement and lawn/garden all had mean distance ratios significantly greater than 1.0, indicating avoidance of these cover types by wood frogs at the 2nd order scale. Bonferonni-corrected pairwise comparisons indicated that water and grass/low shrub were equally preferred when compared to

each other, forest, and tall shrubs, but both were significantly preferred when compared to all other cover categories (Table 3). 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, which examined recorded locations of wood frogs within their home ranges, overall, distances of frogs to cover types differed significantly from distances of random points to these same features ($F_{[9,50]} = 3.80, P = 0.001$). Tall shrubs and bare ground were significantly selected for (i.e., distance ratio significantly differed from 1.0; Table 4); all other cover categories had distance ratios close to 1.0 and were used proportionally to their occurrence within home ranges. Bonferonni-corrected pairwise comparisons indicated that there were no significant differences in selection/avoidance among the nine cover types at the 3rd-order spatial scale (Table 4).

In addition to selection for macrohabitat features, wood frogs demonstrated selection for features at the microhabitat scale, within 1 m² of locations. Sites occupied by frogs were characterized by lower light levels, greater coverage by shrubs, cattail, and open water, and were in closer proximity to water compared to random sites (Table 5). Frog locations were also characterized by significantly lower coverage by grass/forbs compared to paired random sites. We did not detect a significant difference in percent cover by down woody debris, litter, moss and bare ground, vegetation height or soil moisture.

Discussion

As predicted, patterns of movement and habitat use for wood frogs in Edmonton differed from those previously reported in the literature for other populations of the species. Several attributes of our study system likely contribute to these results. Perhaps most important are the differences in climate between Edmonton and the other locations where wood frogs were studied. Average precipitation totals for the months of May to August are 19 to 37 % higher at the study sites in the US (Maine: 335.5 mm and Missouri: 434.3 mm) compared to Edmonton (272.5 mm) (Environment Canada 2016; NOAA 2016). 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; Gabrielsen et al. 2013; Pitt et al. 2017). Within this dry environment, the 11 wetlands included in our study are attractive to anurans as they have permanent hydroperiods and provide constant refuge from desiccation throughout the summer. In Alberta, many permanent water bodies, regardless of size, are shallow (< 2 m deep), freeze to the bottom or exhibit low oxygen levels in winter and thus are fishless or support fluctuating populations of tolerant, small-bodied fishes. Such lakes and wetlands are attractive breeding sites for wood frogs and other anurans sensitive to fish predation, and adults may remain there throughout the summer (Eaton et al. 2005). Distances from the study wetlands to other moist habitat on the landscape (streams, other permanent ponds, more ephemeral wetlands) were large, particularly at the eight urbanized, upland sites which were bounded by narrow, but reliably moist riparian zones of native or semi-natural vegetation.

Movement Patterns and Home Range

The limited number of studies to date that have assessed the migratory movements of amphibians

and reptiles in urban landscapes have produced mixed results. Some studies have demonstrated species undergoing greater migratory movements than observed in natural environments (Montieth and Paton 2006 [spotted salamander, *Ambystoma maculatum* Shaw, 1802]; Harden et al. 2009 [mud turtle, *Kinosternon subrurbrum* Bonaterre, 1789]), whereas others have shown the opposite (Husté et al. 2006 [natterjack toad *Epidalea calamita* Laurent, 1768]). In general, mean and maximum distances travelled by frogs at Edmonton wetlands were low compared to previously reported values during similar periods of the active season (i.e., spring and summer months immediately following breeding) (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a; Freidenfelds et al. 2011). Radio-tracked wood frogs at all our sites were largely confined to habitat immediately surrounding wetlands in which they likely bred. Long-distance migratory movements (maximum distance from wetlands recorded = 122.3 m) were rare, observed for only 10% of individuals, and occurred only in females at the ravine sites which were surrounded by extensive native vegetation. Across all 11 wetlands, female wood frogs moved at higher rates, were relocated, on average, farther from breeding ponds, and made greater maximum excursions from these ponds than males. Other studies have documented adult female wood frogs migrating significantly greater distances from breeding ponds than males during the summer (Regosin et al. 2003), but this difference is not reported for all populations (Rittenhouse and Semlitsch 2007b; Freidenfelds et al. 2011). It has been proposed that female anurans, driven by the high energy requirement of egg production, migrate farther from breeding ponds in search of higher-quality foraging patches (Regosin et al. 2003; Rittenhouse and Semlitsch 2007b). Adult female wood frogs are also less vulnerable to desiccation due to their larger size which could facilitate greater movements from water (Mazerolle and Desrochers 2005).

Avoidance of physiological costs associated with migration by adult wood frogs (i.e., energy consumption and desiccation; Rittenhouse et al. 2009) could be reinforced by the benefits of remaining near wetlands during the short active season in urban, prairie Canada. Heatwole (1961) found that adult wood frogs remained in close proximity (< 1 m) to the perimeter of a Michigan pond, maintaining their locations at the edge as the water-line receded, and only migrating into surrounding forest when the pond fully dried. Radio-tracked golden bell frogs (*Litoria aurea* Lesson, 1827) in Australia also remained in close proximity to permanent constructed wetlands (Garnham et al. 2015).

In the literature, the average adult migration distances for wood frogs is approximately 100 m (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a; Freidenfelds et al. 2011), thus, many of our upland wetlands were potentially too isolated from other moist habitats to allow for true post-breeding migration. The mean distance from upland study wetlands to the closest stream or another wetland was 222.5 ± 90.2 m (range: 38.4 – 876.4 m) and many study sites were surrounded predominantly by inhospitable human-altered habitat. Husté et al. (2006) found that natterjack toad movements among ponds in an urban park in Paris, France were significantly shorter than those observed in natural systems, and breeding adults only moved between waterbodies in close proximity to one another (approximately 80 m). Additionally, wood frogs generally avoid travelling through landscapes with little overhead cover that offer high risks of desiccation and predation (Mazerolle and Desrochers 2005; Regosin et al. 2005; Cline and Hunter 2014). Previous descriptions of wood frog movement patterns, particularly from the northeastern United States (Maine) where vernal pools are abundant and can be used as “stepping stones” by migrating or dispersing amphibians (Freidenfelds et al. 2011; Gabrielsen et

al. 2013; Coster et al. 2015), may not be representative of behaviour across the species' extensive range.

Cross-wetland movements and linear movements along the margins of wetlands led to long, narrow home ranges that were larger in area than the limited movements of tracked frogs away from water would predict (Taylor 2014). We propose that frogs inhabiting the upland stormwater wetlands adopted a strategy of occupying relatively large, but narrow areas, tied to the shorelines of breeding ponds, which supported unmowed strips of natural vegetation. If terrestrial foraging was poor in these edge environments, large home ranges might be required. The ravine wetlands were oxbow ponds within a stream system with an intact, natural riparian zone, but this environment also favoured a pattern of linear movement corridors and home ranges.

Habitat Use

Wood frogs largely remained in and around breeding ponds throughout the tracking period, selecting terrestrial cover types found directly adjacent to ponds (e.g., unmowed grass and patches of shrubs) while avoiding dry areas heavily modified by humans (e.g., buildings and pavement). At the microhabitat level within riparian zones, wood frogs selected for conditions that would reduce water loss (e.g., low light levels, low woody vegetation). Contrary to the species' well-documented existence as a forest obligate in other parts of its range, wood frogs did not significantly select for closed-canopy forest and generally avoided it, even at the three ravine sites where mature aspen and spruce stands were readily accessible adjacent to wetlands.

The presence of open water on the landscape proved to be the most important habitat feature in

explaining wood frog locations at all three habitat scales. Locations of frogs within population ranges and home ranges were consistently closer to open water than predicted based on its availability and individuals used terrestrial microhabitats near standing water and emergent vegetation (i.e., cattails, *Typha latifolia* L., 1753). Besides reducing the risk of desiccation (Baldwin et al. 2006; Rittenhouse et al. 2008), use of shoreline habitat would also allow frogs to avoid terrestrial predators, like garter snakes (*Thamnophis spp.* Fitzinger, 1843) or birds by retreating into the water (Bellis 1965).

Despite the threat of desiccation and predation, we observed wood frogs basking in locations near water. The 3rd-order scale habitat assessment indicated that frogs at all wetlands selected locations within their home ranges that were closer to bare ground than predicted by availability. At the three ravine sites, washouts and sandbars associated with the ponds and adjacent streams were used regularly by several tracked frogs. Active thermoregulation likely plays a role in wood frog behaviour in central Alberta because nights are cool, with average daily low temperatures recorded in 2000 to 2012 at 5° (May), 10° (June, August), and 13° C (July; <http://us.worldweatheronline.com/edmonton-weather-averages/alberta/ca.aspx>). Frogs could exploit sunny, exposed cover types in mornings and evenings to facilitate activity when ambient temperatures are low. Tracked wood frogs in South Carolina were also commonly located along stream banks in tunnels left by decayed tree roots (Pitt et al. 2017).

At constructed wetlands, small islands (< 1500 m²) were important features for wood frogs; nearly 20% of all relocations occurred on them (61 of 341 upland locations). Islands were characterized by tall shrubs, unmowed grass and, at some sites, small patches of trees and open

mats of moss, thus offering protected areas for frogs to forage and bask and avoid terrestrial predators such as domestic cats (Woods et al. 2003).

Wood frogs that did move away from open water typically remained within the grassy riparian zone surrounding wetlands. Over 65% of all frog locations occurred in either grass / low shrub or tall shrub land-cover and both cover types were associated with mean d ratios less than 1.0 at the 2nd and 3rd order spatial scales (tall shrub showing significant selection at both spatial scales, grass/ low shrub only at the 2nd-order scale). Selection for shrub cover was also significant at the microhabitat scale.

Vegetation dominated by tall grasses and shrubs provides leaf litter and downed woody debris, as shelter from predators (Bartelt et al. 2004; Browne 2010), while also facilitating basking and thermoregulation (e.g., mean light transmission recorded at grass / low shrub locations [0.721] was higher than mean light transmission at forest locations [0.411]) (Heinen 1993; Constible et al. 2001; Walsh and Downie 2005). As areas that often contain high invertebrate abundance and diversity (Ferguson 2001; Ferguson and Berube 2004), shrublands likely also provide excellent foraging for wood frogs.

Not surprisingly, wood frogs avoided human structures (i.e., buildings, lawns and gardens, pavement) which provide little in the way of shelter from desiccation or predation (Mazerolle 2001; Mazerolle and Desrochers 2005; Ramirez et al. 2012). Radio-tracked individuals occasionally crossed mowed grass or paved surfaces to reach more suitable areas; however, very few tracked frogs were actually found in yards or lawns, only nine of 563 recorded locations:

seven in garden beds and two in mowed grass. Similarly, Cline and Hunter (2014) reported that, although wood frogs in Maine were capable of dispersing through mowed grass and lawns, they often did so quickly. As all of our relocations were made during daylight hours, we do not know if patterns changed at night; work on nocturnal habitat-use patterns of urban wood frogs and other amphibians is definitely warranted.

In Edmonton, closed-canopy forest was not used selectively by wood frogs compared to other land cover categories. In fact, forest had the highest calculated distance ratio at the 2nd-order spatial scale ($d = 3.65$), although this value was not statistically significantly different from 1.0 so there was no evidence of actual avoidance of forest by wood frogs. Previous studies had identified forest as essential habitat for migration and foraging (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 1), often difficult to access, and isolated from wetlands by patches of bare ground, pavement or mowed grass. Thus, frogs used the shorter shrubby cover that was commonly found closer to water. More surprisingly, despite the prevalence of forest cover at ravine wetlands, wood frogs were rarely located there (18 of 222 locations at ravine wetlands). Although adult wood frogs in eastern North America select forest cover during migratory movements from ephemeral ponds in the spring and fall (Baldwin et al. 2006; Rittenhouse and Semlitsch 2007a), wood frogs in our study system seem to make less use of forest cover during similar periods of their active season. Most individuals tracked at our ravine sites did not migrate and instead remained in close proximity to permanent water in sunnier, more open riparian zones dominated by shrubs or grass.

Management Recommendations

Adult wood frogs at our study wetlands focused their terrestrial activity in narrow (< 20 m wide) strips of shore-side vegetation that lacked a closed canopy and was dominated by shrubs and grasses, but apparently met their requirements for food and shelter during the active season. Although low populations sizes suggest the urban wetlands in our system may be acting as an ecological sink for wood frogs, evidence from genetic and population studies have indicated that successful breeding and recruitment is occurring at many of the wetlands, including upland constructed ponds, and populations have persisted at these sites for several generations (Scheffers and Paszkowski 2013; Furman et al. 2016). Research by Veysey Powell and Babbitt (2015) on wood frogs breeding in ephemeral pools associated with forestry operation in Maine demonstrated that vegetated buffers of 30 m were not sufficient to maintain the abundance and structure of populations at pre-harvest levels, whereas 100 m buffers were sufficient. Abundances of adult and juvenile wood frogs at wetlands within Edmonton, particularly at constructed sites (Scheffers and Paszkowski 2015), are lower than at natural sites in Alberta's aspen parkland (e.g., Anderson et al. 2014) suggesting that the amount of terrestrial habitat available around city ponds limits local population sizes and thus the likelihood of their persistence in the long term. Still it is noteworthy that in 2008, surveys encountered calling male wood frogs at 27 of 58 constructed stormwater wetlands visited within the city limits of Edmonton (Scheffers and Paszkowski 2013). Widening unmowed riparian zones surrounding these wetlands may increase the size, and ultimately the longevity, of these populations. A study of wood frogs at stormwater ponds in Baltimore County, Maryland (Gallagher et al. 2014) encountered calling males at 26 of 68 ponds. Models showed that occupancy was not predicted by the proportion of forest cover in terrestrial buffers of 100, 250 or 500 m surrounding the sites.

Rather, wood frogs appeared reliant on riparian corridors associated with streams that connected the ponds to each other and to patches of natural vegetation, reminiscent of the patterns we documented at our ravine sites.

The lack of accessible, alternative waterbodies on the landscape likely contributed to the limited movements away from upland study wetlands in our system. Waterbodies that do not act as breeding sites (e.g., streams, shallow temporary wetlands) can act as stepping-stones on the landscape for migrating or dispersing amphibians (Semlitsch 2000; Petranka and Holbrook 2006; Okonkwo 2011; Gabrielsen et al. 2013; Pitt et al. 2017). Movement behaviour recorded at our ravine wetlands and other studies indicated 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 2007b; Stevens et al. 2007). The creation of wet drainages or small ponds in proximity to upland amphibian breeding sites could provide additional summering habitat for these animals while also encouraging migration and dispersal (Gabrielsen et al. 2013; Bateman et al. 2015).

Small islands within constructed wetlands appeared to be important habitat features used regularly by wood frogs; nearly 20% of all frog locations (61 of 341 locations) on islands at the three sites where they existed. Islands were characterized by high proportions of tall shrub, unmowed grass and, at some sites, small patches of trees and mats of moss. Creating islands during the construction of urban ponds could benefit wood frog populations whose movements are otherwise confined to the grassy riparian zones of breeding ponds.

An assessment of gene flow in wood frogs from five stormwater and three ravine wetlands in the

current study system found no genetic structure among sites or differences in allelic richness between natural (ravine) and upland constructed wetlands (Furman et al. 2016). These results suggest that an exchange of individuals and genes exists among sites, perhaps through the dispersal of juveniles. The construction or preservation of small patches of long grass, forbs and shrubs at select sites would create stepping stones that assure linkages exist between individual stormwater ponds, and between isolated upland wetlands and the more continuous blocks of natural vegetation represented by the forested ravines that are scattered across the city (see Gallagher et al. 2014). Such simple steps could potentially benefit a variety of wetland invertebrate and vertebrate species in Edmonton and in other cities in prairie Canada. However, social factors like landscape aesthetics, property values, and safety must be integrated into plans and actions aimed at conserving and enhancing biodiversity in urban green spaces (Aronson et al. 2017).

Acknowledgments

We thank Ben Furman, Randi Glen, Stephanie Gour, Jenelle Pelletier, Tyana Rudolfsen, Curtis Vieville and Arthur Whiting for their enthusiasm and hard work in the collection of field data. Invaluable advice and support was also provided by Charlene Nielsen, Bill Tonn, Erin Bayne, Rolf Vinebrook, Brian Eaton, Derek Mackenzie and the PT lab group. Financial and in-kind support for this research came from Alberta Sport, Recreation, Parks and Wildlife Foundation, Natural Sciences and Engineering Research Council (USRA to Stephanie Gour, Discovery Grant to Cindy Paszkowski) and the University of Alberta. Thank you to the City of Edmonton, Strathcona County, and the many landowners at the urban study wetlands.

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Tables

Table 1. Description of land-cover categories used during digitization of landscape surrounding study wetlands and average percentage of total area covered by each land-cover (mean $\pm$ SE) within a 125m buffer around each wetland.

Land-cover	Description	Upland wetlands (% of area)	Ravine wetlands (% of area)
Pavement	Paved surface (road or sidewalk) often associated with high human and automobile traffic	19.5 $\pm$ 1.9	0.1 $\pm$ 0.1
Mowed Grass	City-maintained grass surface, mowed several times throughout the active season	15.2 $\pm$ 2.0	0
Lawn/ Garden	Mix of mowed grass and planted gardens (front and back yards associated with houses)	22.2 $\pm$ 5.0	0
Building	House or other building	15.6 $\pm$ 1.6	0
Water	Open water	8.4 $\pm$ 1.4	6.8 $\pm$ 0.7
Grass/Low Shrub	Unmowed graminoid and low-lying shrubs	7.9 $\pm$ 3.0	9.3 $\pm$ 3.4
Forest	Land-cover dominated by tree species with distinct canopy visible from aerial imagery	7.8 $\pm$ 4.7	75.2 $\pm$ 3.1
Tall Shrub	Shrub cover (often <i>Salix spp.</i>) greater than 3.0 m in height	1.2 $\pm$ 0.5	4.8 $\pm$ 0.1
Bare Ground	Non-vegetated soil (e.g. sandy washout near stream, undeveloped residential lot or gravel walking paths)	2.1 $\pm$ 1.4	3.6 $\pm$ 0.3

Table 2. List of structural and abiotic variables used in the analysis of microhabitat selection by 30 wood frogs (*Lithobates sylvaticus*) 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)

Table 3. Mean distance ratios (d) and Bonferonni-corrected pairwise comparisons (two-tailed t-tests) for 2nd order habitat selection by 30 wood frogs (*Lithobates sylvaticus*) at 11 urban wetlands in Edmonton, Alberta.

Land-cover Category	Mean Distance Ratio ($d=U_i/r_i$) $\pm$ 1SE	Water	Grass/ Low Shrub	Tall Shrub	Bare Ground	Mowed Grass	Building	Pavement	Lawn / Garden
Water	0.2114 $\pm$ 0.05*	-							
Grass/ Low Shrub	0.2754 $\pm$ 0.07*	0.6943	-						
Tall Shrub	0.6159 $\pm$ 0.07*	0.0050	0.0192	-					
Bare Ground	0.8748 $\pm$ 0.13	0.0002	0.0007	0.0928	-				
Mowed Grass	0.9167 $\pm$ 0.09	< 0.0001	< 0.0001	0.0168	0.7901	-			
Building	1.3446 $\pm$ 0.15*	< 0.0001	< 0.0001	0.0001	0.0222	0.0208	-		
Pavement	1.4232 $\pm$ 0.19*	< 0.0001	< 0.0001	0.0003	0.0210	0.0216	0.7553	-	
Lawn/ Garden	1.6177 $\pm$ 0.21*	< 0.0001	< 0.0001	0.0001	0.0048	0.0048	0.3201	0.5142	-
Forest	3.6550 $\pm$ 1.75	0.0605	0.0653	0.0963	0.1279	0.1332	0.2050	0.2215	0.2648

Note: * indicates where mean distance ratios were significantly different from 1.0 at an alpha level of 0.05 ($P < 0.05$).

Statistically significant pairwise comparisons ($P \leq 0.0017$) are presented in bold and indicate where a particular cover type was significantly preferred over another.

Table 4. Mean distance ratios (*d*) and *P*-values from Bonferonni-corrected pairwise comparisons (two-tailed t-tests) for 3rd order habitat selection by 30 wood frogs (*Lithobates sylvaticus*) at 11 urban wetlands in Edmonton, Alberta.

Land-cover Category	Mean Distance Ratio ($d=u_i/r_i$) ± 1SE	Water	Grass/ Low Shrub	Tall Shrub	Bare Ground	Forest	Pavement	Building	Mowed Grass
Water	0.8065 ± 0.11	-							
Grass/ Low Shrub	0.8706 ± 0.09	0.6604	-						
Tall Shrub	0.9019 ± 0.04*	0.4368	0.7598	-					
Bare Ground	0.9126 ± 0.04*	0.3844	0.6788	0.8645	-				
Forest	0.9376 ± 0.04	0.2855	0.5123	0.5773	0.6897	-			
Pavement	0.9594 ± 0.02	0.1898	0.3478	0.2563	0.3371	0.6649	-		
Building	0.9847 ± 0.02	0.1263	0.2265	0.0981	0.1338	0.3420	0.3919	-	
Mowed Grass	0.9942 ± 0.03	0.1127	0.2004	0.0874	0.1179	0.2908	0.3324	0.7842	-
Lawn/ Garden	0.9947 ± 0.02	0.1057	0.1867	0.0600	0.0827	0.2416	0.2091	0.7051	0.1867

Note: * indicates where mean distance ratios were significantly different from 1.0 at an alpha level of 0.05.

Statistically significant pairwise comparisons ($P \leq 0.0017$) are presented in bold and indicate where a particular cover type was significantly preferred over another.

Table 5. Mean microhabitat structure and abiotic measurements at wood frog (*Lithobates sylvaticus*) locations and paired random plots random plots.

Cover Type	Random*	Frog	Wilcoxon <i>P</i> -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

*Cover and abiotic variables are presented as mean values ± 1 SE and (range).

[†] P-values generated from Wilcoxon signed rank test comparing frog use locations to random locations. Values in bold represent statistically significant results (*P*-value ≤ 0.05).

Figure Captions:

Fig. 1. Representative upland wood frog (*Lithobates sylvaticus*) breeding pond in Edmonton, Alberta.

Fig. 2. Representative ravine wood frog (*Lithobates sylvaticus*) breeding pond in Edmonton, Alberta.

Fig. 3. Sample 100% minimum convex polygon (100% MCP) enclosing all frog locations at study wetland 109 with buffered population range. Home ranges calculated using 95% kernel density estimates are also shown for two tracked frogs (Frog 1091 and 1092).

Fig. 4. Mean distance from study wetland (DFW), mean maximum distance from study wetland (MaxDFW) and mean distance per day (DPD) travelled as a function of sex and tracking year for 49 wood frogs (*Lithobates sylvaticus*) radio-tracked at 11 urban wetlands of Edmonton, Alberta. Confidence intervals represent ± 1 SE; sample sizes in parentheses.

Sample 100% minimum convex polygon (100% MCP) enclosing all frog locations at study wetland 109 with buffered population range. Home ranges calculated using 95% kernel density estimates are also shown for two tracked frogs (Frog 1091 and 1092).

1164x899mm (96 x 96 DPI)

Mean distance from study wetland (DFW), mean maximum distance from study wetland (MaxDFW) and mean distance per day (DPD) travelled as a function of sex and tracking year for 49 wood frogs (*Lithobates sylvaticus*) radio-tracked at 11 urban wetlands of Edmonton, Alberta. Confidence intervals represent ± 1 SE; sample sizes in parentheses.

508x508mm (300 x 300 DPI)