Herpetological Conservation and Biology 13(1):113–130.
Submitted: 26 April 2017; Accepted: 16 February 2018; Published 30 April 2018.

Habitat Selection, Movement Patterns, and Hazards Encountered by Northern Leopard Frogs (*Lithobates pipiens*) in an Agricultural Landscape

Melinda G. Knutson[1,2]***, Jennifer H. Herner-Thogmartin***[1,4]***, Wayne E. Thogmartin***[2]***, Joshua M. Kapfer***[3]***, and John C. Nelson***[2]

[1]*U.S. Fish and Wildlife Service, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road, La Crosse, Wisconsin 54603, USA*
[2]*U.S. Geological Survey, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road, La Crosse, Wisconsin 54603, USA*
[3]*University of Wisconsin-Whitewater, Department of Biological Sciences, 352 Upham Hall Whitewater, Wisconsin 53190, USA*
[4]*Corresponding author, email: jennifer_herner-thogmartin@fws.gov*

Abstract.—**Many wildlife species, including frogs, are exposed to hazards in agricultural landscapes. We studied the movements of Northern Leopard Frogs (*Lithobates pipiens*) in southeastern Minnesota, USA, an area with a mix of row crops, hayfields, forests, and riverine wetlands. We tracked Northern Leopard Frogs (n = 59), surgically implanted with radio transmitters, from April to October, 2001–2002. We compared frogs migrating from farm ponds (n = 23) to those migrating from natural wetlands (n = 36) to determine how these frogs differed in their use of the agricultural landscape surrounding these ponds. Irrespective of setting, post-breeding Northern Leopard Frogs most often selected wetlands, followed by grassed areas or forests; row crops (corn or soybeans) were generally avoided. Home ranges were similarly sized in the two settings (range: 4.6 to 5.9 ha). Total distance traveled by radio-tagged frogs ranged from 12–3,316 m and maximum movement per day ranged from 3–396 m. Our data showed that some frogs traveled widely; we observed cross-country movements, across roads and through forests that did not appear to follow existing grassed pathways or corridors. The largest source of known mortality was encounters with agricultural haying equipment (n = 8). We conclude that if wetlands are scarce and pond buffers narrow, Northern Leopard Frogs will use an area up to 6 ha in size and may travel as far as 3 km from the breeding site, traversing multiple land cover types and crossing roads. Presence of grass-dominated corridors may not mitigate migration hazards. In addition to roads and predators, hayfields subject to mowing also present a post-breeding hazard to Northern Leopard Frogs.**

Key Words.—amphibian; Driftless Area; farm pond; home range; radio telemetry; mowing

Introduction

Amphibian populations are declining worldwide (Houlahan et al. 2000; Alford et al. 2001; Johnson et al. 2011), including in industrial agricultural landscapes such as the Midwestern U.S. (Lannoo 1998; Adams et al. 2013), due to habitat loss, disease, fragmentation, introduced species, and pollution. Agricultural intensification is a major threat to amphibian populations primarily because of habitat loss and exposure to agricultural chemicals (Mann et al. 2009). Agriculture is the most common land use globally and is expected to increase in area and intensity as the size of the human population grows (Tilman 2001; Ellis et al. 2010). Agricultural landscapes are expected to face added pressure with increased demand for wind-energy generation and bio-energy feedstocks, resulting in additional loss of natural grasslands (Lu et al. 2009; Dale et al. 2011; Wright and Wimberly 2013). The conservation of declining amphibian populations relies on understanding how amphibians use agricultural landscapes and cultivated grasslands, and identifying the hazards that they face.

A U.S. nation-wide analysis of 45 amphibian species listed the Northern Leopard Frog (*Lithobates pipiens*; Fig. 1) among the top five species with the strongest evidence of population declines over time (Adams et al. 2013). An analysis for the northeast region of the USA also showed significant negative population trends for the Northern Leopard Frog for 2001–2011 (Weir et al. 2014). The Northern Leopard Frog is considered a Species of Greatest Conservation Need in Iowa and Wisconsin (Wisconsin Department of Natural Resources 2005; Reeder and Clymer 2015). A summary of the Iowa Frog and Toad Survey showed the Northern Leopard Frog detected at 12–16% of sites for 2010–2014 with no apparent population declines (Iowa Department of Natural Resources 2014). In Wisconsin, however,

Figure 1. Northern Leopard Frog, *Lithobates pipiens*. (Photographed by Mark F. Roth).

percentage occurrence of the Northern Leopard Frog declined from about 38% to about 25% from 1984 to 2015 (Wisconsin Department of Natural Resources 2015). A petition in 2006 to list the species under the Endangered Species Act resulted in a finding of Not Warranted by the U.S. Fish and Wildlife Service (https://www.fws.gov/midwest/news/463.html [Accessed 17 March 2017]). The species is still considered widespread and relatively common in the eastern U.S and Canada. However, in most western U.S. states and western Canadian provinces, the species is considered sensitive, threatened, or endangered (Germaine and Hays 2009; Johnson et al. 2011; Rogers and Peacock 2012).

Northern Leopard Frogs overwinter in permanent water (bottoms of lakes and streams) and breed early in the spring in southeastern Minnesota (Oldfield and Moriarty 1994). Like other pond-breeding amphibians, Northern Leopard Frogs have a complex life cycle that includes the use of both aquatic and terrestrial habitats (Dole 1965, 1967; Merrell 1970; Semlitsch 2000). Northern Leopard Frogs require different types of water bodies for breeding and overwintering (Merrell 1970); the distances between sites and the potential hazards encountered may influence amphibian migration patterns (Vos and Stumpel 1995; Halley et al. 1996; Semlitsch 2008). This species is highly mobile; post breeding and inter-pond movements are common (Merrell 1970; Dole 1971).

The terrestrial habitats surrounding frog breeding ponds are important during post-breeding for foraging, thermoregulation, dispersal, migration, and overwintering (Baldwin et al. 2006; Rittenhouse et al. 2009). Although natural grasslands are increasingly uncommon in Midwestern agricultural landscapes, hay fields and pastures may act as a surrogate for native prairie grasslands for some amphibian species. Agricultural practices such as annual tillage, fertilizer and pesticide applications, haying, and livestock grazing may influence the suitability of these areas for amphibians (Bonin et al. 1997; Hecnar 1997). In a previous study, we found that agricultural land use was associated with lower anuran abundance and species richness in Iowa but not in Wisconsin (Knutson et al. 1999, 2000), with the differences due to variation in agricultural intensity and landscape context (land cover type and configuration adjacent to the breeding site). Though evidence suggests that some aspects of agricultural land use may be detrimental to anuran populations, we have very little information about how anurans use agricultural landscapes after breeding.

The objective of this study was to assess Northern Leopard Frog movement patterns, home range size, and post-breeding habitat use at three spatial scales, as well as sources of mortality in the agricultural landscape of southeastern Minnesota, and to propose conservation practices to mitigate hazards. A comparison of how constructed farm ponds differ from natural wetlands in this landscape, from the standpoint of use by Northern Leopard Frogs, will inform conservation management of both types of wetlands. The information derived

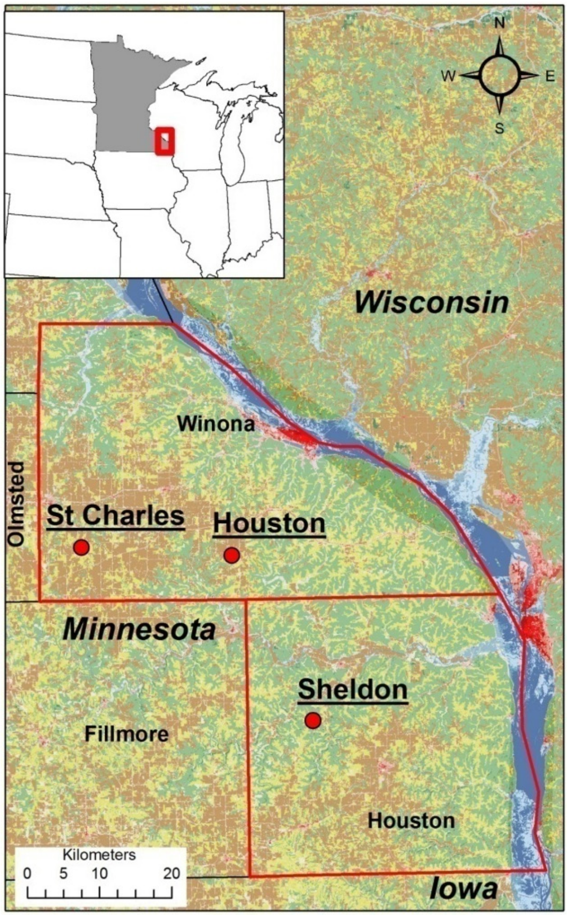

Figure 2. Locations of study sites (red-filled circles) in Houston and Winona counties, Minnesota, USA, 2001 and 2002.

from this study can be applied to conservation decision making, including habitat conservation, restoration, and land acquisition, and perhaps even species reintroductions.

We expected that Northern Leopard Frogs would have larger home ranges and face more hazards when breeding in farm ponds than in natural wetlands because they would need to migrate farther from the farm ponds to seek post-breeding food and shelter. We also anticipated that the primary sources of mortality for frogs using both wetland types would be predation and road crossings (Ashley and Robinson 1996; Vos and Chardon 1998; Lehtinen et al. 1999; Findlay and Bourdages 2000; Mazerolle 2004). We expected that Northern Leopard Frogs would primarily use grassed corridors during movement.

Materials and Methods

Study area.—Southeastern Minnesota falls within Ecoregion 222 Eastern Broadleaf Forest (Continental) Province of Bailey (1995), characterized by Oak-Hickory forests with a lesser component of Maple-Basswood. The region has unique geology that influences land use patterns; it is part of the Driftless Area, characterized by hills and valleys and a mix of agriculture, forests, and small towns (Mickelson et al. 1982; McNab and Avers 1994; Iannicelli 2010). The topography provides a well-drained landscape with few natural wetlands apart from sloughs and oxbows associated with streams and rivers. However, thousands of farm ponds have been constructed in the Driftless Area as a means of soil erosion control and water retention, a conservation practice beginning in the Dust Bowl years of the 1930s and continuing today (Knox 2001). These farm ponds are depressional wetlands with water inflow primarily from precipitation and upslope runoff leading to permanently flooded or intermittently exposed hydrology (Cowardin et al. 1979; Brinson 1993). Some of these constructed farm ponds are used by amphibians for breeding and overwintering (Knutson et al. 2004; Simon et al. 2009; Brand and Snodgrass 2010). However, this agricultural landscape may be hazardous for frogs moving between breeding, feeding, and wintering habitats. Specific information about frog movements, habitat selection, and sources of mortality can be used to inform conservation-focused land management and acquisition.

We conducted field studies of Northern Leopard Frog habitat use and movements at three breeding sites with contrasting wetland characteristics, two constructed farm ponds and one functionally natural riparian wetland, in Houston and Winona counties, in southeastern Minnesota, USA (Fig. 2). The riparian wetland site was located in Winona County, St. Charles Township, Minnesota (43º54’55.49”N, 92º00’41.88”W). This site possessed a 6.30 ha diked wetland composed of grass, sedges, and emergent vegetation, with water inflow from a small stream, surrounded by agricultural land. We tracked Northern Leopard Frogs at this site in 2001 and 2002. Our constructed farm pond study site in 2001 was located in Sheldon Township, Houston County, Minnesota, (43º41’33.81”N, 91º37’13.80”W). In 2002 the constructed farm pond site was located in Hart Township, Winona County, Minnesota (43º88’79.12”N, 91º73’60.50”W). We replaced the Houston County site with the Winona County site in 2002 because the Houston County site provided too few individuals for transmitter implants. The constructed farm pond sites contained ponds with 0.03 and 0.38 ha of wetland, respectively, and were surrounded by a narrow grass buffer and agricultural land. These small sizes are typical of constructed farm ponds in the study area. Our study sites were a subset of 40 randomly selected study sites in a companion amphibian breeding habitat study (Knutson et al. 2004).

We defined our study sites by 1.4-km radius circles centered on the breeding pond. The proportion of land cover types within these areas surrounding the natural wetland and 2002 farm pond sites were similar, with 44–48% grass and 47–43% row crops, respectively, whereas forest represented 8–9% of the site. Wetlands represented 1.06% at the natural wetland site and 0.27% (all constructed) at the 2002 farm pond site. The 2001 farm pond land cover had 64% forest, 30% grass, 6% row crop, and 0.22% wetland (all constructed).

Telemetry methods.—We caught Northern Leopard Frogs by hand and dip net during visual encounter surveys in the spring breeding season. We anesthetized the frogs by placing them in a 3.79 L (1 Gallon) glass jar containing an aqueous solution of 0.02% tricaine methanesulfonate (MS-222, FinquelTM, Argent Chemical Laboratories, Inc., Redmond, Washington, USA) buffered with sodium bicarbonate to pH 7 and kept at room temperature (22–23º C). We surgically implanted radio transmitters (model BD-2GHX, Holohil, Carp, Ontario, Canada; 165 MHz band, 20-week lifetime, 1.85 g) with an internal loop antenna coated with epoxy resin into the peritoneal cavity of frogs weighing > 25 g (Weick et al. 2005). Transmitters represented < 10% of the total weight of the frog (Richards et al. 1994). We implanted transmitters in frogs from April through July and tracked them until October.

We performed the surgeries in the field near the capture site and allowed the frogs to recover for at least 3 h before release at the approximate point of capture (Weick et al. 2005). We tracked the frogs with a receiver (Advanced Telemetry Systems, Isanti, Minnesota, USA) and a hand-held Yagi antenna and we captured geographic coordinates via a hand-held global positioning system (GPS; Rockwell Collins, Inc., Cedar Rapids, Iowa, USA; accuracy about 6.4 m). We detected transmitters at distances ranging from 50–75 m in the field (Weick et al. 2005) and located individual frogs four to five times per week in 2001 and daily in 2002. We tracked frogs from the time of implant until October, or until frogs were lost from tracking (undetected) or transmitters failed. In addition to geographic location, we recorded habitat type and frog health or fate during each observation. We inferred mortality due to predators if we found the frog and/or transmitter with bite marks.

Home range size and habitat selection.—We evaluated seasonal (April-October) home range size, habitat use (time spent in each habitat type), and movement patterns of Northern Leopard Frogs using land-use maps and frog GPS locations within the 1.4-km radius circle centered on the breeding pond. The size of the area was determined based on the patterns of movement we observed in 2001. We interpreted digital maps of land cover with a geographical information system (GIS; ArcView 3.2, Esri, Redlands, California, USA) using infrared aerial photographs taken during summer 2001; we conducted ground truthing in both 2001 and 2002. We classified land uses into four general habitat types: forest, upland grass, row crop, and wetland. Upland grass included pastures, hay fields (alfalfa, clover, or oats), fence rows, road-side ditches and other grass-dominated habitats. Row crops were corn and soybeans. Wetlands comprised open water, flooded grass, and wet meadows. Farmsteads (rural house and associated out-buildings) made up a small portion (< 1%) of the study circles and were considered part of the grass habitat type.

We estimated 95% fixed kernel (area containing 95% of the locations of individuals) and 50% fixed kernel (area containing 50% of the locations of individuals) home range sizes, with the Least Squares Cross Validation (LSCV) smoothing factor incorporated, using the Animal Movement extension V. 2.0 (Hooge and Eichenlaub 1997) for ArcView 3.2 (White and Garrott 1990). Kernel density estimation has been used extensively in field ecological studies and was appropriate for the coarser-resolution data we possessed (Lichti and Swihart 2011). We estimated home ranges for each radio-tagged frog. We excluded Frogs 246 and 726 (from the 2002 farm pond site) from the home range analysis because their estimated home ranges extended outside of the study area. We calculated estimated distances of frog movement using the Create Polyline from Point File function in the Animal Movements extension and subsequently summed the line distances.

We used a log-ratio analysis of habitat compositions (Aebischer et al. 1993; Elston et al. 1996) to determine whether Northern Leopard Frogs selected specific land cover classes within the different landscapes. Land cover proportions x were initially log-ratio transformed ($y_i = \ln(x_i/x_j)$, where x_i is land cover $i = 1,\ldots, D$, $i \neq j$) to create linear independence in the proportions of used land covers (Aebischer et al. 1993). We conducted a multivariate analysis of variance following a ranking matrix of the mean differences between used and available log-ratios to test differences between used and available land cover proportions. For available but unused land cover, we replaced zero land cover proportions by a trivial amount (0.0001). In the case when a land cover was not available for $n \geq 1$ frogs, we used a weighted mean λ, as described in Aebischer et al. (1993), instead of the usual λ.

Habitat selection is a hierarchical process, with food items and forms (4th order) nested within core areas (3rd order), core areas nested within home ranges (2nd order), and home ranges nested within a species range or distribution (1st order; Johnson 1980). We tested three scales of habitat selection. Because we tracked radio-tagged individuals to within approximately 6 m

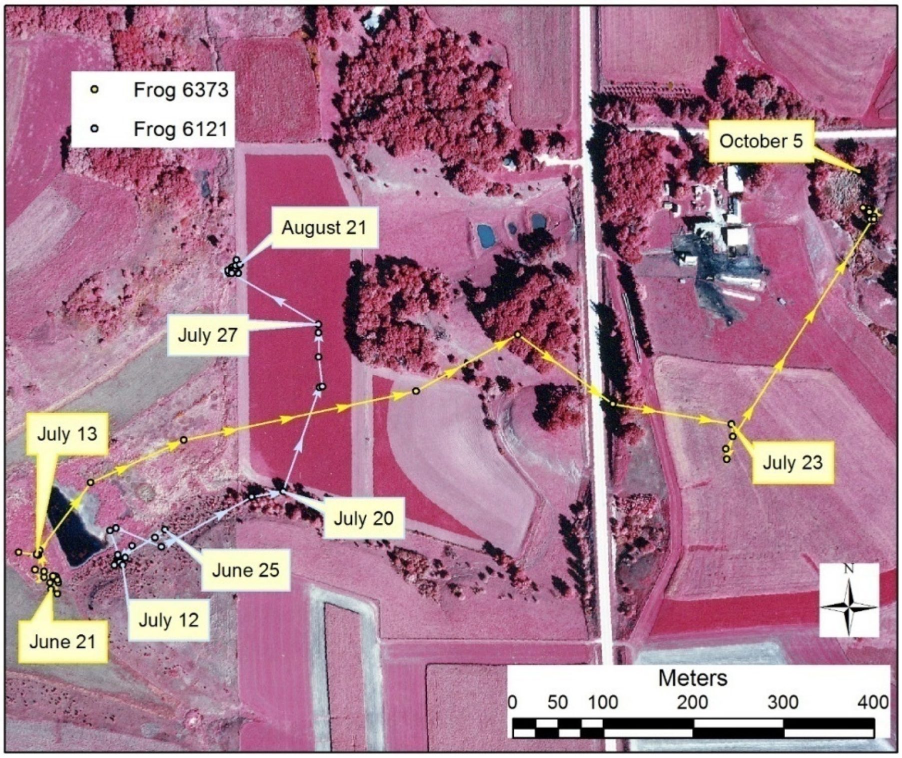

Figure 3. Post-breeding movement patterns of two radio-tracked Northern Leopard Frogs (*Lithobates pipiens*) at the natural wetland site (St. Charles Township, Winona County, Minnesota) in 2001, with a color infrared aerial photograph as background. Movement was from a diked natural wetland (lower left of photo) through various types of cropland where harvest of hay proved fatal for four frogs. Frog #6373 crossed a two-lane pavement road and ended in a small patch of trees near a stream. (Photographed by Brian R. Lubinski).

of their exact location during each observation, the land cover type occupied by these frogs was easily verified. Therefore, we were able to compare the proportion of each land cover type used by telemetered frogs and the proportion of each land cover type that was available to the frogs. We similarly assessed the 50% core area of the Northern Leopard Frogs against the 95% fixed kernel home ranges. Lastly, we assessed the 95% fixed kernel home ranges against that available within the study area. These multiple scales of analysis describe Northern Leopard Frog microsite selection (4th order habitat selection), habitat use within their operational area (3rd order habitat selection), and population response to available habitat in the landscape (2nd order habitat selection; Johnson 1980).

We summarized and graphed population-level relative differences in use and availability as geometric mean selection ratios ($w_i = o_i/\pi_i$, where i indicates the i^{th} land cover, oi is the used proportion, and π_i is the available proportion in land cover i; Pendleton et al. 1998). These selection indices do not account for the unit sum constraint and thus are not independent summaries of selection for each land cover, but they do correspond well with compositional analysis rankings (Pendleton et al. 1998). We used the adehabitat package (version 1.3; Calenge 2006) in R (version 2.0.1; Ihaka and Gentleman 1996) for all habitat selection calculations; the significance threshold for all hypothesis tests was set at $\alpha = 0.05$.

Results

Frog movement and home range.—We tracked 59 frogs; 24 frogs (natural wetland, n = 17; farm pond, n = 7) in 2001 and 35 frogs (natural wetland, n = 19; farm pond, n = 16) in 2002 (Appendix). We tracked frogs from 2–178 d with the average of 50 d. We tracked 10 of the 59 frogs until October. None of the frogs were tracked in multiple years.

Of the 59 frogs implanted with transmitters, 26 frogs were lost from tracking, and transmitters failed in five cases (Table 1, Appendix). Eight mortalities occurred due to encounters with agricultural equipment (hay mowing); four mortalities occurred from predation, and eight occurred for unknown reasons. Eight frogs survived until the last day tracked in October.

At the natural wetland site, nine of 17 frogs in 2001 and six of 18 frogs in 2002 remained in the wetland area near the capture pond; the remaining frogs migrated away from the breeding pond (Fig. 3). At the farm pond sites, we also observed migration beyond the capture pond. At the 2001 farm pond site, all seven frogs

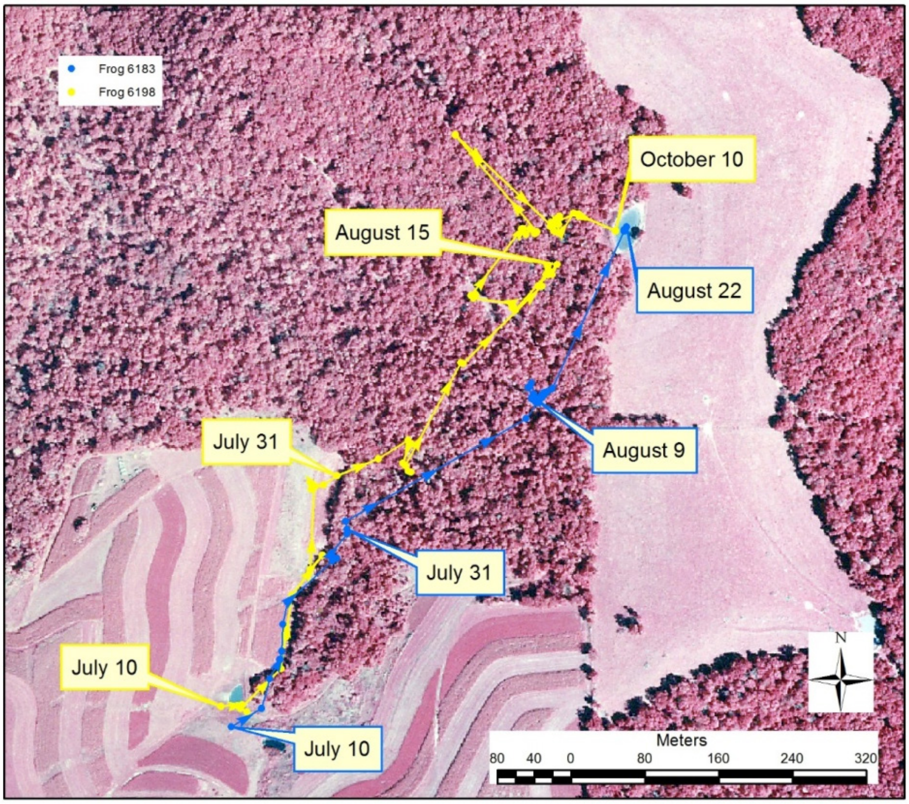

Figure 4. Post-breeding movement patterns of two radio-tracked Northern Leopard Frogs (*Lithobates pipiens*) at 2001 farm pond site (Sheldon Township, Houston County, Minnesota), with a color infrared aerial photograph as background. The movement was from the breeding site (lower left) to another farm pond, requiring movement down-slope, then upslope through forest to the second pond. The timing suggests that frog #6198 may have overwintered at the second pond. (Photographed by Brian R. Lubinski).

migrated beyond a 0.3 ha area consisting of the capture pond and a thin grass buffer. This site had a large wooded area to the north of the pond that four frogs occupied (Fig. 4). At the 2002 farm pond site, four of the 16 frogs ventured away from the capture pond. This site contained a farm pond and a narrow grass buffer to form a 0.38 ha area surrounded on all sides by large patches of row crops and hay fields (Fig. 5). One of the four frogs that ventured away from the 2002 farm pond where it was captured was still alive at the end of the study; two of the four perished due to mowing of hay fields, and the other was lost from tracking with its last location in a hay field.

The patterns of movement illustrate that the migrating frogs at both the natural wetland and the constructed farm ponds crossed all available land cover types and roads (Figs. 3–5). The migrating frog movements appeared directed towards other farm ponds (the frogs seemed to know where they were going) and they did not stay within grassed cover types as they traversed the study area, even when such corridors were available.

During the course of this study, we tracked 10 frogs into October. However, two frogs at the natural wetland site in 2002 were lost from tracking with their last locations in pasture and flooded grass. The other eight frogs survived until the last day tracked in October of each year (natural wetland, 2001, n = 4; 2002, n = 1; farm pond, 2001, n = 2; 2002, n = 1). At the natural wetland in 2001, we made final seasonal (October) location determinations for two of the four frogs near the capture pond; the third frog traveled 400 m north of

Table 1. Number of radio tracked Northern Leopard Frogs (*Lithobates pipiens*) by site, year, and fate, for study sites in Houston and Winona counties, Minnesota, USA, 2001 and 2002.

Fate	Natural 2001	Natural 2002	Farm Pond 2001	Farm Pond 2002	Total
Mortality, unknown cause	2	0	1	5	8
Depredation	0	2	0	2	4
Mower	4	2	0	2	8
Transmitter failure	1	1	1	2	5
Missing*	6	13	3	4	26
Survived to last day tracked	4	1	2	1	8
Total	17	19	7	16	59

*Lost from tracking (undetected)

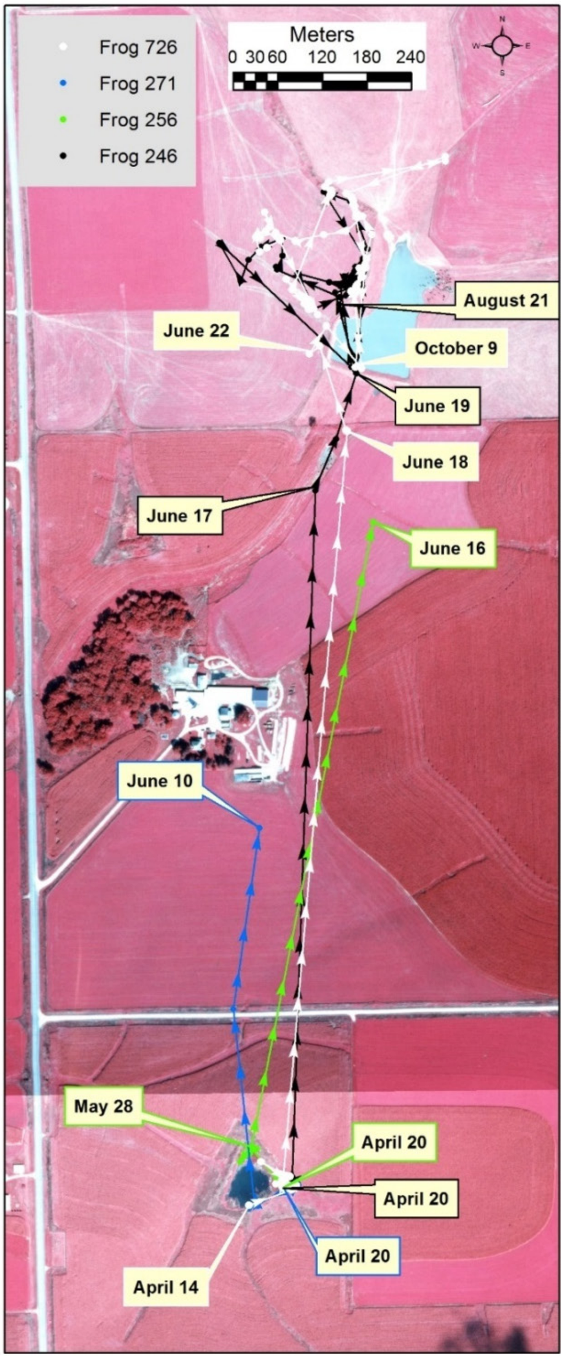

Figure 5. Post-breeding movement patterns of radio-tracked Northern Leopard Frogs (*Lithobates pipiens*) at the 2002 farm pond site (Hart Township, Winona County, Minnesota), with a color infrared aerial photograph as background. Only four frogs dispersed from capture pond in the south and traveled north across row crops and hay fields toward a large pond 1,100 m from capture pond. Frog #271 perished due to the harvest of a hay field and Frog #256 perished in a hay field. Frog #246 made it to the large pond but was lost from tracking in August. The last location was in a hay field. Frog #726 was tracked until the end of the study and the timing suggests that it may have overwintered at the second pond. (Photographed by Brian R. Lubinski).

the capture pond to an area close to a smaller pond; and the fourth frog traveled 950 m east across agricultural hay fields, into a small patch of trees, across a country road, through additional row crops and hay fields, to another pond (Frog 6373; Fig. 3). In 2002 at the natural wetland, the final seasonal (October) location was near the capture pond for the one frog surviving until the end of the study. At the farm pond in 2001, we documented a final seasonal (October) location for one frog near the capture pond and one frog travelled to a different farm pond 650 m to the north. This frog traveled through a large forest patch to get to the second pond (Frog 6198; Fig. 4). In 2002 at the farm pond, we documented the final seasonal (October) location for one frog at a large farm pond 1,128 m to the north (Frog 726; Fig. 5). The total distance traveled by radio-tagged frogs ranged from 12–3,316 m and maximum movement per day was 3–396 m (Table 2). The mean movement per day exhibited by radio-tagged frogs was 15 ± (SE) 1.3 m (Table 2).

Estimated 95% fixed kernel home ranges for all sites and all years varied from 0.0091–42.6 ha ($\bar{x}$ = 5.3 ± [SE] 1.2 ha) whereas 50% core areas varied from 0.0015–9.20 ha ($\bar{x}$ = 1.05 ± 0.3 ha; Table 2). Irrespective of setting and contrary to our expectations, Northern Leopard Frogs used similar sized areas; at the natural wetland site, the average 95% home range area was 4.60 ha in 2001 and 5.88 ha in 2002 (Table 3) whereas the 2001 and 2002 farm pond sites averaged 5.43 ha and 4.84 ha, respectively (Table 3). Average 50% core areas at the natural wetland site were 0.92 ha in 2001 and 1.23 ha in 2002 whereas core areas were 0.68 ha at the 2001 farm pond site and 1.10 ha at the 2002 farm pond site (Table 3).

Mortality.—All mortalities due to agricultural equipment occurred during hay (alfalfa or clover) mowing events in June through August. At the natural wetland site, six radio-tagged frogs were killed by agricultural equipment when hayfields were mowed in 2001 and 2002. In addition, at the 2002 farm pond site, two frogs perished due to haying operations. Pastures were present only at our natural wetland site and we documented no mortality from cattle. We could not definitely identify predator species except in one of the four predation events; an American Bittern (*Botaurus lentiginosus*) was observed eating a frog with a transmitter at the 2002 farm pond site.

Habitat selection.—Log-ratio analyses revealed that tracked Northern Leopard Frogs demonstrated non-random selection of habitat types at all sites regardless of year, and at all levels of selection (2nd, 3rd, and 4th orders), with few exceptions (Table 4; Fig. 6). Northern Leopard Frogs disproportionately selected wetland

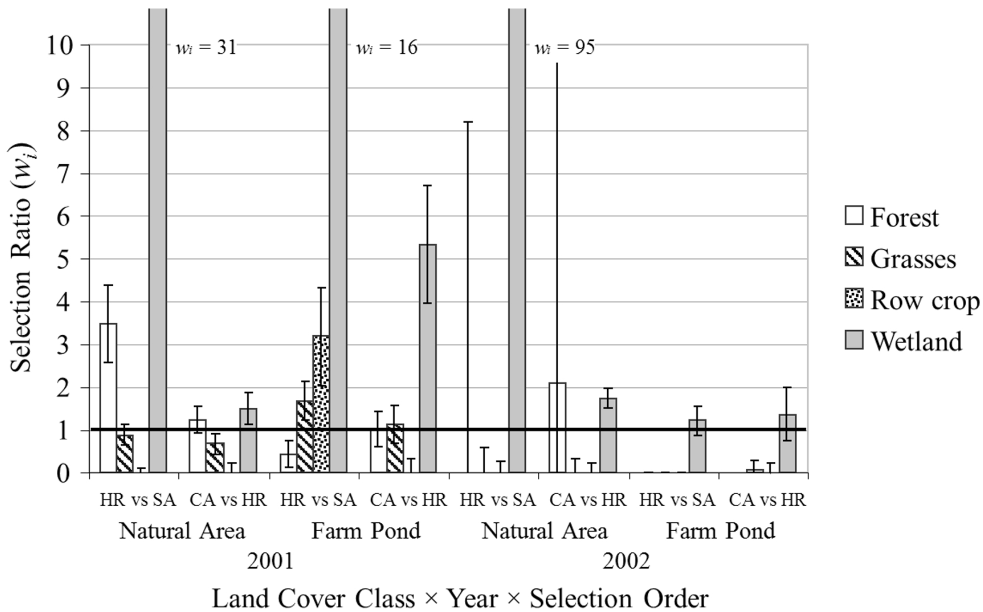

Figure 6. Selection ratios (w_i; used proportion/available proportion) by study location, year, and selection order, summed over the sample of Northern Leopard Frogs (*Lithobates pipiens*), southeastern Minnesota, USA. Abbreviations are SA = study area, HR = home range, and CA = core area. Vertical bars indicate the 95% confidence intervals around the means. The bold line at a selection ratio of one indicates selection used is in proportion to availability.

over all other land cover classes. The results for the other three land cover classes were mixed, varying over space and time. Grassland, ranging between 30% and 48% among the three study sites, was either used proportionate to availability or avoided. At the 2001 farm pond site, where forest cover was 64%, Northern Leopard Frogs used forest less than expected; however, forest was also used less than expected at 2002 farm pond site, where forest comprised 9% of the land cover.

Table 2. Mean, standard error (SE), median, minimum (Min), and maximum (Max) of Northern Leopard Frog (*Lithobates pipiens*) weights, movements, and home ranges for study sites in Houston and Winona counties, Minnesota, USA, 2001 and 2002. The asterisk (*) indicates frogs in 2001 that were not tracked daily; movements averaged over multiple days.

Parameter	Mean	SE	Median	Min	Max
Locations (n)	31	2.9	25	3	89
Weight (g)	44	1.4	40	30	79
Min. distance (m)	2	0.8	1	0	48
Max. distance (m)	184	27	131	6	1026
Total distance (m)	719	84.1	648	12	3316
Mean distance (m)	27	4.4	19	3	259
Tracking duration (d)	50	4.9	46	2	178
Min. movement/day (m)*	1	0.5	0	0	28
Max. movement/day (m)*	93	9.9	81	3	396
Mean movement/day (m)*	15	1.3	13	1	47
95% Home range (ha)	5.3	1.2	1.5	0.009	42.6
50% Core area (ha)	1.0	0.3	0.2	0.002	9.2

Row crop agriculture was generally avoided irrespective of setting.

At the coarsest order of selection (2nd order) considered in this study, Northern Leopard Frogs were similarly situated with respect to habitat, irrespective of setting. Home ranges were placed non-randomly with respect to the 2001 farm pond ($\lambda = 0.037$, $P = 0.018$, n = 7), 2002 farm pond ($\lambda = 0.0005$, $P = 0.001$, n = 14) and the natural wetland (2001: $\lambda = 0.106$, $P = 0.001$, n = 17; 2002: $\lambda = 0.345$, $P = 0.001$, n = 19) sites (Table 4; Fig. 6). Wetlands were selected for in each landscape except in the 2002 farm pond site, where wetlands were used in proportion to their availability. Row crop was avoided in both years at all sites. The response to forest and grass was mixed across years and sites.

Within home ranges, habitat use within core use areas (3rd order) varied considerably. Core use areas were non-randomly placed at the natural wetland site in 2001 ($\lambda = 0.172$, $P = 0.008$, n = 17), but not in 2002 ($\lambda = 0.643$, $P = 0.411$, n = 19; Table 4; Fig. 6). Wetland habitat was favored and row crop avoided at the natural wetland site. Conversely, no selection of core areas occurred at the 2001 farm pond site ($\lambda = 0.408$, $P = 0.198$, n = 7), whereas wetlands were used as available but grass and row crop were avoided at the 2002 farm pond site ($\lambda = 0.263$, $P = 0.002$, n = 14).

At the finest order of selection (4th order), we found individual frog locations within landscapes were placed non-randomly for three of the four study location-year combinations (Table 4). Northern Leopard

Table 3. Average kernel home range and core area (ha) including sample size (n) of Northern Leopard Frogs (*Lithobates pipiens*) by land cover type and total for study sites in Houston and Winona counties, Minnesota, USA, 2001 and 2002.

Area	Pond	Year	n	Forest (ha)	Grasses (ha)	Row Crop (ha)	Wetland (ha)	Total (ha)
95% home range area	Natural	2001	17	0.74	1.81	1.01	1.04	4.60
	Farm pond	2001	7	3.13	1.65	0.56	0.10	5.43
	Natural	2002	19	1.00	2.10	1.51	1.26	5.88
	Farm pond	2002	16	0.00	2.65	1.90	0.29	4.84
50% core area	Natural	2001	17	0.19	0.24	0.13	0.35	0.92
	Farm pond	2001	7	0.43	0.19	0.04	0.02	0.68
	Natural	2002	19	0.23	0.40	0.29	0.32	1.23
	Farm pond	2002	16	0.00	0.81	0.09	0.20	1.10

Frog locations at the natural wetland site occurred non-randomly in both years (2001: Wilks' λ = 0.027, Randomized P = 0.001, n = 17; 2002: λ = 0.157, P = 0.001, n = 19). Only at the 2002 farm pond site did Northern Leopard Frog locations occur selectively (λ = 0.028, P = 0.002, n = 14) and Northern Leopard Frogs at the 2001 farm pond site were distributed according to the availability of habitat (λ = 0.901, P = 1.000, n = 7).

During an extended dry period in 2001, we observed that frogs at the natural wetland and farm pond sites remained in close proximity to capture ponds. Frogs that migrated beyond the areas around the capture ponds in 2001 did so only after the first rainfall. In 2002, rainfall was more regular and the migration date was more variable. During the same time period in 2002, under wetter conditions, frogs had larger home ranges and exploited different land covers. Frogs also exploited new habitats and expanded their home range size in 2001 after the first rainfall in 25 d.

Discussion

Frog use of an agricultural landscape.—Agriculture dominates a large portion of the geographic range of the Northern Leopard Frog, yet very little information is available about post-breeding habitat use and movement in agricultural landscapes (but see Bartelt and Klaver 2017). Our study is the first to describe how Northern Leopard Frogs use constructed compared with natural wetlands, moving within a landscape dominated by row crop agriculture. From a conservation standpoint, it is important to understand how this species uses agricultural landscapes and what hazards are encountered there.

Contrary to our expectations, habitat use and home range sizes were similar between our natural wetland and farm pond sites. We attribute this similarity to the small proportion of wetlands in comparison to other land uses at all of our study sites, farm pond or natural wetland. Wetlands comprised a very small proportion

Table 4. Simplified ranks for habitat selection of Northern Leopard Frogs (*Lithobates pipiens*) for study sites in Houston and Winona counties, Minnesota, USA, 2001 and 2002. Ranks are based upon randomized P-values.

Study Area, Year	Level of Selection	Land Cover Rankings[a]
Natural Area, 2001	Individual Locations vs. Study Area	WET FOR GRS RCP
Farm Pond, 2001	Individual Locations vs. Study Area	No Selection
Natural Area, 2002	Individual Locations vs. Study Area	WET GRS FOR RCP
Farm Pond, 2002	Individual Locations vs. Study Area	WET GRS RCP FOR
Natural Area, 2001	Core Use Area vs. Home Range	WET FOR GRS RCP
Farm Pond, 2001	Core Use Area vs. Home Range	No Selection
Natural Area, 2002	Core Use Area vs. Home Range	No Selection
Farm Pond, 2002	Core Use Area vs. Home Range	WET GRS RCP[b]
Natural Area, 2001	Home Range vs. Study Area	WET FOR GRS RCP
Farm Pond, 2001	Home Range vs. Study Area	WET RCP GRS FOR
Natural Area, 2002	Home Range vs. Study Area	WET FOR GRS RCP
Farm Pond, 2002	Home Range vs. Study Area	WET GRS RCP FOR

[a]From most favored to least favored. WET = wetland, GRS = grasses, FOR = forest, and RCP = row crop.
[b]Forest not occupied by Northern Leopard Frogs in 2002.

of our study sites (≤ 1%), even for our natural wetland. This is typical of the Driftless Area and many other locations in the agricultural Midwest. Northern Leopard Frogs typically migrate seasonally from breeding ponds to spend most of their time in grasslands, fields, pastures, and damp woods (Dole 1965; Merrell 1970). At all three of our study sites, many frog locations post-breeding were in the wetlands surrounding a pond. The frogs preferred wetlands, but they also used grasslands and forests and avoided row crops. Some frogs migrated total distances of up to 3 km from the breeding pond, crossing roads, row crops, hay fields, and woodlands. This implies that all of their needs were not met by these small areas of wetland. In contrast, Bartelt and Klaver (2017) found that most Northern Leopard Frogs in their study remained in close proximity to breeding ponds, which were surrounded by ≥ 20 ha of restored tall-grass prairie.

Long-distance movement of Northern Leopard Frogs has been observed in other studies. Merrell (1970) believed frogs traveled up to 3,218 m to overwintering locations in Minnesota; Hine et al. (1981) reported a frog that moved 400 m in five days. Bartelt and Klaver (2017) report straight line distance movements ranging from 31–857 m. Blomquist and Hunter (2009) documented an average home range size of 0.11 ha (range, 0.0013–0.84 ha) for post-breeding Northern Leopard Frogs occupying a mixed coniferous-deciduous forest in Maine, an order of magnitude smaller than our results (mean 95% home range = 5.3 ha). However, the landscape context and purpose of their study differed from ours and they tracked frogs for only 1 mo post-breeding (16 May-18 June 2006).

The general pattern for the frogs included in this study, at all scales of selection, was a selection (not surprisingly) for wetland above all other cover types, and a general avoidance of row crop agriculture. Only at the coarsest scale of selection, the home range relative to the study area, was row crop selected over that of grassland or forest, and then only at the farm pond site, perhaps a consequence of proximity rather than preference. Forest was generally selected over that of grassland, but this finding was inconsistent, particularly at the finest scale of selection. Bartelt and Klaver (2017) also found strong selection for wetland by Northern Leopard Frogs and avoidance of row crops.

Leopard Frogs rely on deep-water refuge during droughts (Lannoo 2005). Other studies suggest that frog movements follow the contours of the landscape that hold moisture (Merrell 1970; Dole 1971; Hine et al. 1981). Our observations of longer amphibian movements and an increase in home range size after a rain following a drought is consistent with literature indicating that amphibians tend to migrate greater distances after a rain or when moisture levels are high (Dole 1965; Pope et al. 2000; Mazerolle 2001; Blomquist and Hunter 2009).

Contrary to our expectations, Northern Leopard Frogs not only travelled extended distances, but through all available habitat types; we had expected them to occupy primarily wetlands and grasslands. Grassed buffers along rivers and streams provide multiple conservation benefits (Lee et al. 2003; Muenz et al. 2006), but our data indicate that frogs do not always follow these corridors. We observed direct cross-country movements that did not follow any existing grassed pathways and the movement paths did not appear to be impeded by roads, forests, or row crops (i.e., corn, soy beans). Indeed, the pattern of movements for several frogs that migrated away from the breeding pond suggests that the frogs knew their destinations (another pond) and they moved in that direction, crossing whatever lay between them and their destinations. Similar patterns of direct movement across multiple land cover types have been documented for California Red-legged Frogs (*Rana draytonii*; Bulger et al. 2003). In contrast, Bartelt and Klaver (2017) found that Northern Leopard Frogs avoided crossing row crops and instead frequented roadside ditches or grassy banks along streams.

Breeding sites can be different than wintering sites. When migrating from their breeding ponds, most of the frogs included in this study traveled to other ponds or streams. This occurred at all three study sites with distances traveled to ponds away from the breeding ponds ranging from 300–1,100 m. We tracked some frogs late enough into the fall to suggest that they used one pond for breeding and a different pond for overwintering. Such behavior was implied in several other tracked individuals that were headed for adjacent ponds, but either died or were lost from tracking en route. This type of movement (from breeding ponds to overwintering areas) has been documented in other anuran studies as well (Merrell 1970; Matthews and Pope 1999). The relatively large number of frogs that were lost from tracking may be related to the long distances the frogs included in this study tended to travel away from the breeding pond. The relatively short transmitter detection distance (50–75 m), combined with logistical constraints (few roads, rough terrain, multiple private landowners) that required tracking all frogs by foot, made detection unlikely if the frogs migrated beyond the 1.4-km radius circle centered on the breeding pond.

Hazards.—The agricultural landscape can be hazardous for frogs due to encounters with domestic and native predators (cats, birds, etc.), as well as farming activities such as hay mowing, cattle grazing, and crop tillage. Contrary to our expectations, more mortalities were documented due to haying operations (eight mortalities) than to road crossings (zero) or predation (four). We observed six frogs crossing roads with no mortalities, probably because the roads in our study area were rural with a low volume of vehicular traffic. However, many other studies have demonstrated that road mortality is a hazard for frogs (Ashley and Robinson 1996; Vos and Chardon 1998; Lehtinen et al. 1999; Findlay and Bourdages 2000; Mazerolle 2004). We documented four instances of predation; domestic cats, snakes, and birds have been documented as terrestrial predators of frogs (Murray et al. 2004; Loyd et al. 2013).

Mazerolle and Desrochers (2005) reported that Northern Leopard Frogs avoid disturbed landscapes (peat mines, agricultural land, or recently cut forest stands) during movement. However, the frogs in our study readily occupied agricultural hay fields adjacent to breeding ponds, exposing them to mortality from haying equipment. Bartelt and Klaver (2017) also documented mortality due to mowing and crushing by agricultural equipment as well as predation. Studies of habitat quality using data from multiple ponds indicate that disturbances such as mowing, grazing, and logging in the vicinity of the wetland can negatively affect amphibian populations (Stapanian et al. 2015). Research on turtles in agricultural landscapes indicates that mortality risk in grasslands can be mitigated in part via the choice of mowing equipment (sickle bar mowers result in less mortality) and mowing height, but the risk of crushing by tractor tires remains difficult to mitigate (Erb and Jones 2011).

Some Midwestern farmers delay mowing of hayfields until a certain date (usually 15 July) to benefit grassland birds, which allows chicks to fledge from the nest (Vickery et al. 2000). Unfortunately, the no-mowing period for Northern Leopard Frogs would need to extend over the entire growing season to avoid risk. Our data do not reveal any safe time during the growing season when mowing would not affect the frogs. However, grasslands managed for conservation do need periodic management (mowing, grazing, or burning) to control shrub and tree invasion. Among these options, periodic, low intensity grazing may present the least risk to amphibians (Burton et al. 2009). The hazards associated with grazing vary by amphibian species (Larson 2014; Kay et al. 2017).

We conclude that if wetlands are scarce and pond buffers narrow, Northern Leopard Frogs will use an area up to 6 ha in size and may travel as far as 3 km away from the breeding site, traversing multiple land cover types and crossing roads. The presence of grass-dominated corridors may not necessarily mitigate migration hazards. In addition to roads and predators, hayfields subject to mowing also pose a hazard to Northern Leopard Frogs. Movement patterns suggest that some frogs were breeding in one pond and over-wintering in another location, although we lack conclusive evidence for this.

Management considerations for public land managers.—When acquiring or managing land for conservation, public land managers could consider the specific life histories and hazards encountered by amphibians in addition to the usual considerations for birds and mammals. Key aspects to consider may include the safety of wetlands or grass-dominated areas adjacent to breeding sites and potential travel routes among wetlands < 3 km distant that may be used for either breeding or over-wintering (Semlitsch 1998; Maisonneuve and Rioux 2001; Semlitsch and Bodie 2003; Mazerolle 2005; Baldwin et al. 2006). Management activities such as mowing and haying adjacent to breeding sites can be avoided or minimized if Northern Leopard Frogs are expected to occupy the site. In addition, new wetland acquisitions should avoid heavily travelled roads, if possible. If such hazards cannot be avoided, managers could consider ways to mitigate the hazards (road underpasses, restrictions on mowing, wide grassed buffer strips surrounding breeding sites, or adjacent land acquisition).

Landscapes that include large wetland complexes provide all of the requirements needed by Northern Leopard Frogs for survival including food, shelter, breeding, and overwintering areas and are a priority for conservation acquisitions or easements. In agricultural regions, conserving natural habitats, such as grasslands and forests, while also reducing crop field size and configuration, will benefit most amphibians (Collins and Fahrig 2017). For example, Balas et al. (2012) found that Northern Leopard Frogs and several other anuran species were more likely to occupy sites in native prairies and conservation grasslands than farmed wetlands in the Prairie Pothole Region. A mix of shallow ponds that warm faster in the spring for breeding and ponds deep enough to avoid freezing to the bottom over the winter will provide an adequate mix of habitats. Wetlands adjacent to small creeks and streams, similar to our natural wetland site, also benefit overwintering anurans by providing frost-free aquatic habitats.

Management considerations for private landowners and farmers.—Our data show that Northern Leopard Frogs and agriculture can co-exist, but finding ways to minimize hazards will benefit this species. In the Driftless Area, the unique topography provides opportunities for diverse forms of agriculture (e.g., cattle grazing, vegetables, grapes, apples, and honey production) that may be less hazardous to frogs than traditional row crop agriculture. However, the same topography also favors hay production, which we found to be hazardous for Northern Leopard Frogs post-breeding. Companion amphibian research focused on the Driftless Area showed that farm ponds used for watering livestock had elevated concentrations of phosphorus and nitrogen, higher turbidity, and a trend toward reduced amphibian reproductive success compared to natural ponds (Knutson et al. 2004).

General management practices that benefit most amphibians include protecting the wetland breeding site by keeping nitrogen levels low, excluding fish or refraining from stocking fish, and maintaining some open water during the spring and early summer (Knutson et al. 2004). Ideally, nitrogen levels should be < 0.5 mg/L (Knutson et al. 2004). The best way to achieve this is by excluding cattle and other grazing animals from direct access to the wetland and maintaining grass buffer strips > 200 m wide (Castelle et al. 1994, Semlitsch 1998; Bartelt and Klaver 2017).

Management practices such as hay mowing are particularly hazardous to Northern Leopard Frogs; they cannot escape fast or far enough to avoid crushing or entanglement in mowing equipment. There is little information on hazards presented by cattle grazing, but grazing is almost certainly less hazardous to frogs than mowing; frogs can more easily escape grazers than mowing equipment (Burton et al. 2009). Therefore, in addition to a wide grassed buffer strip immediately surrounding the breeding pond, frog-friendly agricultural land uses in proximity to the wetland include grazed grassland and woodlots.

Acknowledgments.—We thank the private landowners who allowed us to work on their land. Funding was provided by the Amphibian Research and Monitoring Initiative of the U.S. Geological Survey, the Minnesota Environment and Natural Resources Trust Fund (as recommended by the Legislative Commission on Minnesota Resources), the Milwaukee Zoological Society, and the University of Wisconsin-La Crosse. We thank Shawn Weick, Brian Pember, Brent Knights, Winona State University, Neal Mundahl, Robert Drieslein, Fred Kollmann, Kevin Kenow, Larry Robinson, Meredith Kline, Bart Bly, Joel Jahimiak, Sam Bourassa, Ben Campbell, Andy Kimball, John Moriarty, Pete Boma, and Kara Vick for assistance. The study was approved by the Animal Care and Use Committee of the U.S. Geological Survey (USGS), Upper Midwest Environmental Sciences Center (UMESC). Amphibian care and handling were conducted under USGS UMESC Standard Operating Procedure No. 417.0; surgical procedures followed USGS UMESC Standard Operating Procedure TS416.0. Work was conducted under Minnesota Department of Natural Resources Special Collection Permits No. 9516 and 10870. Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. Department of the Interior, U.S. Geological Survey, or the U.S. Fish and Wildlife Service. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Literature Cited

Adams, M.J., D.A.W. Miller, E. Muths, P.S. Corn, E.H.C. Grant, L.L. Bailey, G.M. Fellers, R.N. Fisher, W.J. Sadinski, H. Waddle, et al. 2013. Trends in amphibian occupancy in the United States. PloS ONE 8:e64347. https://doi.org/10.1371/journal.pone.0064347

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Alford, R.A., P.M. Dixon, and J.H.K. Pechmann. 2001. Global amphibian population declines. Nature 412:499–500.

Ashley, E.P., and J.T. Robinson. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. Canadian Field Naturalist 110:403–412.

Bailey, R.G. 1995. Description of the ecoregions of the United States, 2nd Edition. U.S. Forest Service Miscellaneous Publication 1391. Washington, D.C., USA. 108 p.

Balas, C.J., N.H. Euliss, and D.M. Mushet. 2012. Influence of conservation programs on amphibians using seasonal wetlands in the Prairie Pothole Region. Wetlands 32:333–345.

Baldwin, R.F., A.J. Calhoun, and P.G. deMaynadier. 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the Wood Frog (*Rana sylvatica*). Journal of Herpetology 40:442–453.

Bartelt, P.E., and R.W. Klaver. 2017. Response of anurans to wetland restoration on a midwestern agricultural landscape. Journal of Herpetology 51:504–514.

Blomquist, S.M., and M.L. Hunter, Jr. 2009. A multi-scale assessment of habitat selection and movement patterns by Northern Leopard Frogs (*Lithobates* [*Rana*] *pipiens*) in a managed forest. Herpetological Conservation and Biology 4:142–160.

Bonin, J., M. Ouellet, J. Rodrigue, J.L. DesGranges, F. Gagne, T.F. Sharbel, and L.A. Lowcock. 1997. Measuring the health of frogs in agricultural habitats subjected to pesticides. Pp. 246–257 *In* Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation. Green, D.M. (Ed.).

Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA.

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

Brinson, M.M. 1993. A hydrogeomorphic classification for wetlands. U.S. Army Corps of Engineers Wetlands Research Program Technical Report WRP-DE-4. Washington, D.C., USA. 79 p.

Bulger, J.B., N.J. Scott, and R.B. Seymour. 2003. Terrestrial activity and conservation of adult California Red-legged Frogs *Rana aurora draytonii* in coastal forests and grasslands. Biological Conservation 110:85–95.

Burton, E.C., M.J. Gray, A.C. Schmutzer, and D.L. Miller. 2009. Differential responses of postmetamorphic amphibians to cattle grazing in wetlands. Journal of Wildlife Management 73:269–277.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Castelle, A.J., A.W. Johnson, and C. Conolly. 1994. Wetland and stream buffer size requirements: a review. Journal of Environmental Quality 23:878–882.

Collins, S.J., and L. Fahrig. 2017. Responses of anurans to composition and configuration of agricultural landscapes. Agriculture, Ecosystems & Environment 239:399–409.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service FWS/OBS 79/31. Washington, D.C., USA. 131 p.

Dale, V.H., K.L. Kline, L.L. Wright, R.D. Perlack, M. Downing, and R.L. Graham. 2011. Interactions among bioenergy feedstock choices, landscape dynamics, and land use. Ecological Applications 21:1039–1054.

Dole, J.W. 1965. Summer movements of adult Leopard Frogs, *Rana pipiens* Schreber, in northern Michigan. Ecology 46:236–255.

Dole, J.W. 1967. Spring movements of Leopard Frogs, *Rana pipiens* Schreber, in northern Michigan. Amerian Midland Naturalist 78:167–181.

Dole, J.W. 1971. Dispersal of recently metamorphosed Leopard Frogs, *Rana pipiens*. Copeia 1971:221–228.

Ellis, E.C., K. Klein Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589–606.

Elston, D.A., A.W. Illius, and I.J. Gordon. 1996. Assessment of preference among a range of options using log ratio analysis. Ecology 77:2538–2548.

Erb, L., and M.T. Jones. 2011. Can turtle mortality be reduced in managed fields? Northeastern Naturalist 18:489–496.

Findlay, C.S., and J. Bourdages. 2000. Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology 14:86–94.

Germaine, S.S., and D.W. Hays. 2009. Distribution and postbreeding environmental relationships of Northern Leopard Frogs (*Rana* [*Lithobates*] *pipiens*) in Washington. Western North American Naturalist 69:537–547.

Halley, J.M., R.S. Oldham, and J.W. Arntzen. 1996. Predicting the persistence of amphibian populations with the help of a spatial model. Journal of Applied Ecology 33:455–470.

Hecnar, S.J. 1997. Amphibian pond communities in southwestern Ontario. Pp. 1–15 *In* Amphibians in Decline: Canadian Studies of a Global Problem. Herpetological Conservation. Green, D.M. (Ed.). Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA.

Hine, R.L., B.F. Hellmich, and B.L. Les. 1981. Leopard Frog populations and mortality in Wisconsin, 1974–76. Wisconsin Department of Natural Resources Technical Bulletin 122. Madison, Wisconsin, USA. 39 p.

Hooge, P.N., and B. Eichenlaub. 1997. Animal movement extensions to Arcview, version 1.1. Alaska Biological Science Center, U.S. Department of the Interior, Geological Survey, Anchorage, Alaska.

Houlahan, J.E., C.S. Findlay, B.R. Schmidt, A.H. Meyer, and S.L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature 404:752–755.

Iannicelli, M. 2010. Evolution of the Driftless Area and contiguous regions of Midwestern USA through Pleistocene periglacial processes. Open Geology Journal 4:35–54.

Ihaka, I., and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299–314.

Iowa Department of Natural Resources. 2014. Iowa's Frog and Toad Survey 2014. Iowa Department of Natural Resources, Des Moines, Iowa, USA. 7 p.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, P.T.J., V.J. McKenzie, A.C. Peterson, J.L. Kerby, J. Brown, A.R. Blaustein, and T. Jackson. 2011. Regional decline of an iconic amphibian associated with elevation, land-use change, and invasive species. Conservation Biology 25:556–566.

Kay, G.M., A. Mortelliti, A. Tulloch, P. Barton, D. Florance, S.A. Cunningham, and D.B. Lindenmayer. 2017. Effects of past and present livestock grazing on herpetofauna in a landscape-scale experiment. Conservation Biology 31:446–458.

Knox, J.C. 2001. Agricultural influence on landscape sensitivity in the Upper Mississippi River Valley. Catena 42:193–224.

Knutson, M.G., W.B. Richardson, D.M. Reineke, B.R. Gray, J.R. Parmelee, and S.E. Weick. 2004. Agricultural ponds support amphibian populations. Ecological Applications 14:669–684.

Knutson, M.G., J.R. Sauer, D.A. Olsen, M.J. Mossman, L.M. Hemesath, and M.J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. Conservation Biology 13:1437–1446.

Knutson, M.G., J.R. Sauer, D.O. Olsen, M.J. Mossman, L.H. Hemesath, and M.J. Lannoo. 2000. Landscape associations of frog and toad species in Iowa and Wisconsin, USA. Journal of the Iowa Academy of Sciences 107:134–145.

Lannoo, M.J. (Ed.) 1998. Status and Conservation of Midwestern Amphibians. University of Iowa Press, Iowa City, Iowa, USA.

Lannoo, M.J. 2005. Amphibian Declines: the Conservation Status of United States Species. University of California Press, Berkeley, California, USA.

Larson, D.M. 2014. Grassland fire and cattle grazing regulate reptile and amphibian assembly among patches. Environmental Management 54:1434–1444.

Lee, K.H., T.M. Isenhart, and R.C. Schultz. 2003. Sediment and nutrient removal in an established multi-species riparian buffer. Journal of Soil and Water Conservation 58:1–8.

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

Lichti, N.I., and R.K. Swihart. 2011. Estimating utilization distributions with kernel versus local convex hull methods. Journal of Wildlife Management 75:413–422.

Loyd, K.A.T., S.M. Hernandez, J.P. Carroll, K.J. Abernathy, and G.J. Marshall. 2013. Quantifying free-roaming domestic cat predation using animal-borne video cameras. Biological Conservation 160:183–189.

Lu, X., M.B. McElroy, and J. Kiviluoma. 2009. Global potential for wind-generated electricity. Proceedings of the National Academy of Sciences 106:10933–10938.

Maisonneuve, C., and S. Rioux. 2001. Importance of riparian habitats for small mammal and herpetofaunal communities in agricultural landscapes of southern Québec. Agriculture, Ecosystems & Environment 83:165–175.

Mann, R.M., R.V. Hyne, C.B. Choung, and S.P. Wilson. 2009. Amphibians and agricultural chemicals: review of the risks in a complex environment. Environmental Pollution 157:2903–2927.

Matthews, K.R., and K.L. Pope. 1999. A telemetric study of the movement patterns and habitat use of *Rana muscosa*, the Mountain Yellow-legged Frog, in a high-elevation basin in Kings Canyon National Park, California. Journal of Herpetology 33:615–624.

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

Mazerolle, M.J. 2004. Amphibian road mortality in response to nightly variations in traffic intensity. Herpetologica 60:45–53.

Mazerolle, M.J. 2005. Drainage ditches facilitate frog movements in a hostile landscape. Landscape Ecology 20:579–590.

Mazerolle, M.J., and A. Desrochers. 2005. Landscape resistance to frog movements. Canadian Journal of Zoology 83:455–464.

McNab, W.H., and P.E. Avers. 1994. Ecological Subregions of the United States. U.S. Forest Service WO-WSA-5. Washington, D.C., USA.

Merrell, D.J. 1970. Migration and gene dispersal in *Rana pipiens*. American Zoologist 10:47–52.

Mickelson, D., J. Knox, and L. Clayton. 1982. Glaciation of the Driftless Area: an evaluation of the evidence. Pp. 155–169 *In* Quaternary History of the Driftless Area. Ostrom, M.E. (Ed.). Geological and Natural History Survey, University of Wisconsin-Extension, Madison, Wisconsin, USA.

Muenz, T.K., S.W. Golladay, G. Vellidis, and L.L. Smith. 2006. Stream buffer effectiveness in an agriculturally influenced area, southwestern Georgia: responses of water quality, macroinvertebrates, and amphibians. Journal of Environmental Quality 35:1924–1938.

Murray, D.L., J.D. Roth, and A.J. Wirsing. 2004. Predation risk avoidance by terrestrial amphibians: the role of prey experience and vulnerability to native and exotic predators. Ethology 110:635–647.

Oldfield, B., and J.J. Moriarty. 1994. Amphibians and Reptiles Native to Minnesota. University of Minnesota Press, Minneapolis, Minnesota, USA.

Pendleton, G.W., K. Titus, E. DeGayner, C.J. Flatten, and R.E. Lowell. 1998. Compositional analysis and GIS for study of resource selection by Goshawks in southeast Alaska. Journal of Agricultural, Biological, and Environmental Statistics 3:280–295.

Pope, S.E., L. Fahrig, and N.G. Merriam. 2000. Landscape complementation and metapopulation effects on Leopard Frog populations. Ecology 81:2498–2508.

Reeder, K., and J. Clymer (Eds.). 2015. Iowa Wildlife Action Plan: securing a future for fish and wildlife - a conservation legacy for Iowans. Iowa Department of Natural Resources, Des Moines, Iowa, USA.

Richards, S.J., U. Sinsch, and R.A. Alford. 1994. Supplemental approaches to studying amphibian biodiversity: radio tracking. Pp. 155–158 *In* Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.A.C. Hayek, and M.S. Foster (Eds). Smithsonian Institution Press, Washington, D.C., USA.

Rittenhouse, T.A.G., R.D. Semlitsch, and F.R. Thompson. 2009. Survival costs associated with Wood Frog breeding migrations: effects of timber harvest and drought. Ecology 90:1620–1630.

Rogers, S.D., and M.M. Peacock. 2012. The disappearing Northern Leopard Frog (*Lithobates pipiens*): conservation genetics and implications for remnant populations in western Nevada. Ecology and Evolution 2:2040–2056.

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

Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615–631.

Semlitsch, R.D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72:260–267.

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

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

Stapanian, M.A., M. Micacchion, and J.V. Adams. 2015. Wetland habitat disturbance best predicts metrics of an amphibian index of biotic integrity. Ecological Indicators 56:237–242.

Tilman, D. 2001. Effects of diversity and composition on grassland stability and productivity. Pp. 183–207 *In* Ecology: Achievement and Challenge. Press, M.C., N.J. Huntly, and S. Levin (Eds). Blackwell Science, Oxford, England.

Vickery, P.D., J.R. Herkert, F.L. Knopf, J. Ruth, and C.E. Keller. 2000. Grassland birds: an overview of threats and recommended management strategies. Pp. 74–77 *In* Strategies for Bird Conservation: The Partners in Flight Planning Process. Proceedings of the 3rd Partners in Flight Workshop, Cape May, New Jersey, October 1–5, 1995. USDA Forest Service Proceedings RMRS-P-1. U.S. Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Vos, C.C., and J.P. Chardon. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the Moor Frog *Rana arvalis*. Journal of Applied Ecology 35:44–56.

Vos, C.C., and A.H.P. Stumpel. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landscape Ecology 11:203–214.

Weick, S.E., M.G. Knutson, B.C. Knights, and B.C. Pember. 2005. A comparison of internal and external radio transmitters with Northern Leopard Frogs (*Rana pipiens*). Herpetological Review 36:415–421.

Weir, L.A., A. Royle, K.D. Gazenski, and O. Villena. 2014. Northeast regional and state trends in anuran occupancy from calling survey data (2001–2011) from the North American Amphibian Monitoring Program. Herpetological Conservation and Biology 9:223–245.

White, G.C., and R.A. Garrott. 1990. Analysis of Wildlife Radio-tracking Data. Academic Press, New York, New York, USA.

Wisconsin Department of Natural Resources. 2005. Wisconsin's strategy for wildlife species of greatest conservation need. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

Wisconsin Department of Natural Resources. 2015. Frog and toad survey 2015. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA. 9 p.

Wright, C.K., and M.C. Wimberly. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proceedings of the National Academy of Sciences 110:4134–4139.

Melinda G. Knutson is an Ecologist and owner of Trillium Consulting, LLC. When this research was conducted, she was a Research Wildlife Biologist with the U.S. Geological Survey at the Upper Midwest Environmental Sciences Center in La Crosse, Wisconsin. From 2005–2017 she worked as a Regional Biologist for the U.S. Fish and Wildlife Service, leading the Inventory and Monitoring Branch in the Division of Natural Resources and Conservation Planning in the Midwest Region. Her primary interests are conservation biology of birds and amphibians, natural resources decision making, monitoring, and adaptive management. She retired from federal service in 2017. (Photographed by David L. Ford).

Jennifer H. Herner-Thogmartin is a Biologist working with the U.S. Fish and Wildlife Service (USFWS), Midwest Region at the Upper Midwest Environmental Sciences Center in La Crosse, Wisconsin. She earned her Master's of Science in Biology at the University of Arkansas, Fayetteville, and her Bachelors of Science in Zoology from the University of Washington, Seattle. Currently, she assists in writing inventory and monitoring and habitat management plans for USFWS Region 3 refuges. Her interests are in avian ecology, wildlife conservation, and habitat management. (Photographed by Wayne E. Thogmartin).

Wayne E. Thogmartin is a quantitative ecologist with the U.S. Geological Survey at the Upper Midwest Environmental Sciences Center in La Crosse, Wisconsin. His research occurs principally at the intersection of animal ecology, spatial analyses, and statistics. His interests are in population ecology for animals declining in abundance, asking new questions of multiple, combined data sets to gain novel insight into the dynamics of animal populations, and translating science into guidance for practical management decisions. (Photographed by Robert J. Kratt).

Joshua M. Kapfer (pictured here uploading temperature logger data from an Ornate Box Turtle, *Terrapene ornata*) is a Certified Wildlife Biologist® with The Wildlife Society and an Associate Professor in the Department of Biological Sciences at the University of Wisconsin-Whitewater. Josh has nearly two decades of professional experience working with wildlife and is primarily interested in their ecology and conservation. He has numerous peer-reviewed publications on topics ranging from aggressive behavior and sexual selection in fish to the habitat preferences and spatial ecology of upper Midwestern reptiles. He has also mentored many undergraduate research students that have gone on to professional careers in the fields of ecology and conservation. (Photographed by Joseph Mozuch).

John C. (JC) Nelson is currently the Data Manager for the U.S. Geological Survey, Upper Midwest Environmental Sciences Center in La Crosse, Wisconsin. He has been part of the Geospatial Sciences and Technologies Branch working in various positions for many years. His current research interests include data integration, visualization, and accessibility. (Photographed by Robert J. Kratt).

Appendix. Rates of movement (m/day) and distance traveled (m) by *Lithobates pipiens* at study sites in Houston and Winona Counties, Minnesota, 2001 and 2002 (Sheldon = 2001 farm pond site; Houston = 2002 farm pond site; St. Charles = 2001 and 2002 natural wetland site). We used only frogs with at least three tracking locations. Wt = weight. Date format is YYYYMMDD where Y = year, M = month, D = day.

Site	Frog ID	Wt (g)	Start date	End date	Number of Locations (n)	Min. dist. (m)	Max. dist. (m)	Total dist. (m)	Mean dist. (m)	Days tracked	Min. move rate (m/day)	Max. move rate (m/day)	Mean move rate (m/day)	95% Home range (m^2)	50% Core area (m^2)	Fate*
Sheldon	6495	55	20010601	20010720	37	1	396	1634	45	49	1	396	33	16688	4863	MS
Sheldon	6520	79	20010612	20010906	64	1	135	1131	18	86	0	81	13	25312	1766	TF
Sheldon	6630	44	20010705	20010802	21	3	148	755	38	28	3	105	27	39837	4021	MS
Sheldon	6646	51	20010705	20011015	72	0	103	1326	19	105	0	67	13	7052	868	SE
Sheldon	6183	56	20010710	20010822	29	0	225	798	29	43	0	113	19	125844	14703	UM
Sheldon	6198	42	20010710	20011018	69	0	154	1593	23	100	0	137	16	115581	12032	SE
Sheldon	6558	67	20010710	20010906	44	0	277	1113	26	58	0	102	19	50079	9544	MS
St. Charles	6478	39	20010515	20010702	38	0	91	552	15	48	0	91	11	3904	860	MS
St. Charles	6530	46	20010611	20010727	36	2	104	423	12	46	2	104	9	10596	2071	MS
St. Charles	6546	37	20010611	20010730	35	3	164	848	25	49	2	82	17	26203	4281	MO
St. Charles	6558	39	20010611	20010619	4	48	156	259	259	8	28	48	32	59125	11493	MO
St. Charles	6220	57	20010614	20010620	6	0	21	31	6	6	0	21	5	490	97	UM
St. Charles	6593	61	20010614	20010901	59	1	81	791	14	79	1	62	10	21384	4133	TF
St. Charles	6358	36	20010615	20010803	37	1	61	488	14	49	1	61	10	7517	860	MS
St. Charles	6373	44	20010621	20011018	46	0	304	1540	34	119	0	263	13	426485	92084	SE
St. Charles	6620	55	20010621	20010713	16	2	81	296	20	22	2	81	13	7915	1468	MS
St. Charles	6104	42	20010625	20011018	69	0	146	736	11	115	0	73	6	5882	783	SE
St. Charles	6121	64	20010625	20010821	38	1	122	779	21	57	0	114	14	69743	14237	MS
St. Charles	6133	45	20010628	20011015	67	0	152	837	13	109	0	152	8	2391	516	SE
St. Charles	6147	69	20010628	20011018	62	0	419	1033	17	112	0	30	9	26724	5681	SE
St. Charles	6155	41	20010628	20010716	12	8	153	568	52	18	4	153	32	10361	1701	MS
St. Charles	6383	37	20010628	20010810	31	0	94	779	26	43	0	94	14	6930	1050	UM
St. Charles	6403	37	20010628	20010726	19	1	179	648	36	28	1	142	23	78118	11646	MO
St. Charles	6207	53	20010716	20010731	12	0	86	247	22	15	0	42	16	17752	3069	MO
Houston	694	39	20020414	20020603	26	1	53	328	13	50	0	44	7	2495	321	TF
Houston	726	41	20020414	20021009	89	0	1026	3316	38	178	0	119	19	397444	71393	SE
Houston	740	37	20020414	20020513	13	2	64	153	13	29	1	32	5	943	222	TF
Houston	797	39	20020414	20020501	9	1	47	138	17	17	1	24	8	2381	391	DE

Site	Frog ID	Wt (g)	Start date	End date	Number of Locations (n)	Min. dist. (m)	Max. dist. (m)	Total dist. (m)	Mean dist. (m)	Days tracked	Min. move rate (m/day)	Max. move rate (m/day)	Mean move rate (m/day)	95% Home range (m^2)	50% Core area (m^2)	Fate*
Houston	821	39	20020415	20020515	15	1	39	116	8	30	1	39	4	543	128	UM
Houston	846	41	20020415	20020531	24	0	45	250	11	46	0	33	5	4409	684	MS
Houston	869	38	20020415	20020422	6	7	16	56	11	7	5	13	8	726	168	UM
Houston	132	35	20020417	20020531	23	0	17	105	5	44	0	16	2	213	23	DE
Houston	423	35	20020417	20020419	3	6	10	16	8	2	6	10	8	334	114	UM
Houston	978	36	20020417	20020603	24	1	156	398	17	47	0	56	8	3017	547	MS
Houston	246	33	20020419	20020821	84	0	928	3056	37	124	0	155	25	363237	85494	MS
Houston	256	32	20020419	20020616	19	0	860	1031	57	58	0	65	18	36967	13565	MO
Houston	271	38	20020419	20020610	23	0	265	660	30	52	0	66	13	15023	4568	MO
Houston	283	35	20020419	20020429	5	4	38	68	17	10	1	19	7	1580	821	UM
Houston	423_2	36	20020419	20020427	5	0	6	12	3	8	0	3	1	98	15	UM
Houston	756	35	20020503	20020510	3	4	9	13	7	7	1	3	2	199	54	MS
St. Charles	677	38	20020418	20020717	63	0	95	949	15	90	0	95	11	6228	662	MS
St. Charles	736	52	20020418	20020627	40	0	172	1164	30	70	0	172	17	69160	7667	TF
St. Charles	891	40	20020418	20020617	35	0	107	579	17	60	0	107	10	2517	445	MS
St. Charles	714	32	20020424	20020621	29	0	100	387	14	58	0	50	7	697	173	MS
St. Charles	857	33	20020522	20020617	19	2	41	287	16	26	2	41	11	4506	735	MS
St. Charles	831	40	20020612	20020711	23	3	313	1267	58	29	3	313	44	86598	13228	MS
St. Charles	869	40	20020612	20021004	76	0	229	1253	17	114	0	119	11	59104	14315	MS
St. Charles	970	30	20020612	20020708	25	2	111	735	31	26	2	111	28	158146	49573	MS
St. Charles	998	50	20020612	20020812	28	1	321	889	33	61	1	161	15	98674	24189	MO
St. Charles	930	32	20020625	20020707	9	3	330	565	71	12	3	133	47	165409	25181	MS
St. Charles	894	34	20020702	20020802	18	1	312	512	30	31	1	45	17	19719	3625	MO
St. Charles	756	41	20020718	20020810	22	1	250	892	42	23	1	250	39	194249	51056	MS
St. Charles	821	47	20020718	20020810	23	0	131	522	24	23	0	131	23	50247	8569	MS
St. Charles	920	72	20020718	20020819	31	0	183	721	24	32	0	183	23	61018	9509	MS
St. Charles	183	65	20020725	20021004	33	1	396	1174	37	71	1	99	17	54123	7851	MS
St. Charles	221	50	20020725	20020812	9	1	15	35	4	18	0	15	2	91	18	DE
St. Charles	432	39	20020725	20020729	5	1	26	42	10	4	1	26	10	693	129	MS
St. Charles	891_2	51	20020725	20020821	23	0	16	120	5	27	0	16	4	520	108	DE
St. Charles	955	39	20020725	20021004	34	0	255	1391	42	71	0	139	20	84997	17382	SE

*Fate: UM = Unknown mortality (n = 8), MS = Missing (lost from tracking; n = 26), TF = Transmitter failure (n = 5), SE = Survived to last day tracked (n = 8), MO = Mower mortality (n = 8), DE = Depredation (n = 4)