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Response of Anurans to Wetland Restoration on a Midwestern Agricultural Landscape

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ABSTRACT.—**Since the early 1990s, >5,000 ha of historic wetlands (and adjacent prairie) have been restored on the row-crop agricultural landscape of Winnebago County, Iowa, USA. From 2008–2011, we surveyed 22 of these sites for probabilities of occupancy and colonization by Boreal Chorus Frogs (BCF; *Pseudacris maculata*), Northern Leopard Frogs (NLF; *Lithobates pipiens*), and American Toads (AT; *Anaxyrus americanus*). We used radio telemetry to measure patterns of movement and habitat use by 22 NLF and 54 AT and deployed biophysical models in available habitats to estimate their physiological costs. The BCF occupied 100% of restored wetlands; NLF and AT occupied 59–91% and 71–89%, respectively, varying according to annual weather conditions. The BCF colonized new sites within a year; NLF and AT required 3 and 2 yr, respectively. These differences were related to distances from the nearest established population and costs of intervening cover types, and were statistically related to the size and orientation of restored wetlands. The ranges of maximum straight-line distances moved by NLF and AT were 31–857 m and 42–2,932 m, respectively. Both NLF and AT selected wetlands and surrounding prairies, though NLF were nine times more likely to select wetland habitats than all others combined. About 24% of AT used row-crop fields extensively, but not until crops had grown sufficiently to reduce the physiological costs of these fields similar to that of prairies. Both BCF and AT navigated the dramatically altered row-crop landscape, but NLF depended more heavily on roadside ditches to find and colonize restored wetlands.**

Historic wetlands in Winnebago County, Iowa, USA were largely shallow, ephemeral ponds (Prior, 1991) that supported amphibian populations (Lannoo, 1996). After ~150 yr of wetland drainage and plowing, Iowa has lost >99% of its prairie and wetlands (Samuels, 2009). Habitat loss is recognized as a major factor contributing to declines in amphibian populations (e.g., Halliday, 2005) and, in the Midwest United States, agriculture has been the primary source of this change (Leja, 1998).

Wetland restoration can abate habitat loss and amphibians can respond well to wetland restoration, sometimes recolonizing quickly (e.g., ≤5 yr; Pechmann et al., 2001). Restoring such wetlands (e.g., by destroying drainage tile) can recreate their historic hydroperiods and facilitate successful recolonization by comparable amphibian communities (Brodman, 2006; Reeves et al., 2016; Stiles et al., 2016).

The impact of wetland restoration on amphibian populations on agricultural landscapes has received some attention (e.g., Lehtinen and Galatowitsch 2001; Wen, 2015), but recolonization on landscapes of almost continuous row-crop monocultures remains poorly understood. Winnebago County in north-central Iowa is dominated by such a landscape. Beginning in the 1990s and using funds provided by the Wetland Reserves Program, the United States Department of Agriculture's Natural Resources Conservation Service (NRCS) has worked with landowners to restore poorly drained farm land back to wetlands (www.nrcs.usda.gov/wps/portal/nrcs/detail/national/about/history/?cid=nrcs143_021392). Through the collaborative efforts of the Iowa Department of Natural Resources (DNR), Winnebago County Conservation Board (WCCB), and private landowners, >5,000 ha among hundreds of individual wetlands have been restored since the early 1990s (Schwarz, pers. comm.). These restored wetlands often are separated by kilometers of cropland and, because amphibians have limited vagility (Sinsch, 1990; Driscoll, 1998; Semlitsch, 1998), successful colonization requires movement corridors of suitable habitat that increase landscape connectivity (Rothermel, 2004; Mazerolle and Desrochers, 2005; Stiles et al., 2016).

Corridors in Midwestern agricultural landscapes are especially important to amphibians because they are wet-skinned ectotherms with little or no physiological control over evaporative water loss. They are sensitive to thermal gradients and vulnerable to exposed, low-humidity environments (Shoemaker et al., 1992), a condition found in row-crop fields for much of the active season. In addition, the Midwestern agricultural landscape is dissected by roads that can slow or prevent the dispersal of some amphibians (Fahrig et al., 1995; Lehtinen et al., 1999); hence, these landscapes can present considerable resistance to amphibian dispersal (Semlitsch, 2000). Understanding how amphibians navigate these landscapes, use available habitats, and respond to different patterns of wetland sizes, shapes, and juxtaposition will provide important information for developing more-effective conservation plans for these important animals.

Our goal in this study was to measure the response of anuran populations to "islands" of restored wetlands across a row-crop agricultural matrix. Specifically, we wanted to know: 1) How many recently (i.e., in the last 20 yr) restored wetlands are occupied by anurans? 2) How much time is required for anurans to recolonize a newly restored wetland? 3) What paths across the agricultural landscape do anurans follow when dispersing to newly restored wetlands? and 4) What landscape features facilitate the dispersal of anurans across the agricultural landscape?

Our working hypotheses were: 1) A majority of recently restored wetlands will be colonized by at least one species of anuran; 2) following the nearest neighbor hypothesis (Clark and Evans, 1954) and the theory of island biography (MacArthur and Wilson, 1967), we expect the time required to colonize newly restored wetlands to be directly related to the distance to the nearest established wetland; and 3) based on the physiological limitations of anurans, we expect these animals to select paths that minimize rates of evaporative water loss.

MATERIALS AND METHODS

We surveyed a set of restored wetlands from spring through fall of 2008–2011. Specifically, we estimated occupancy and rates

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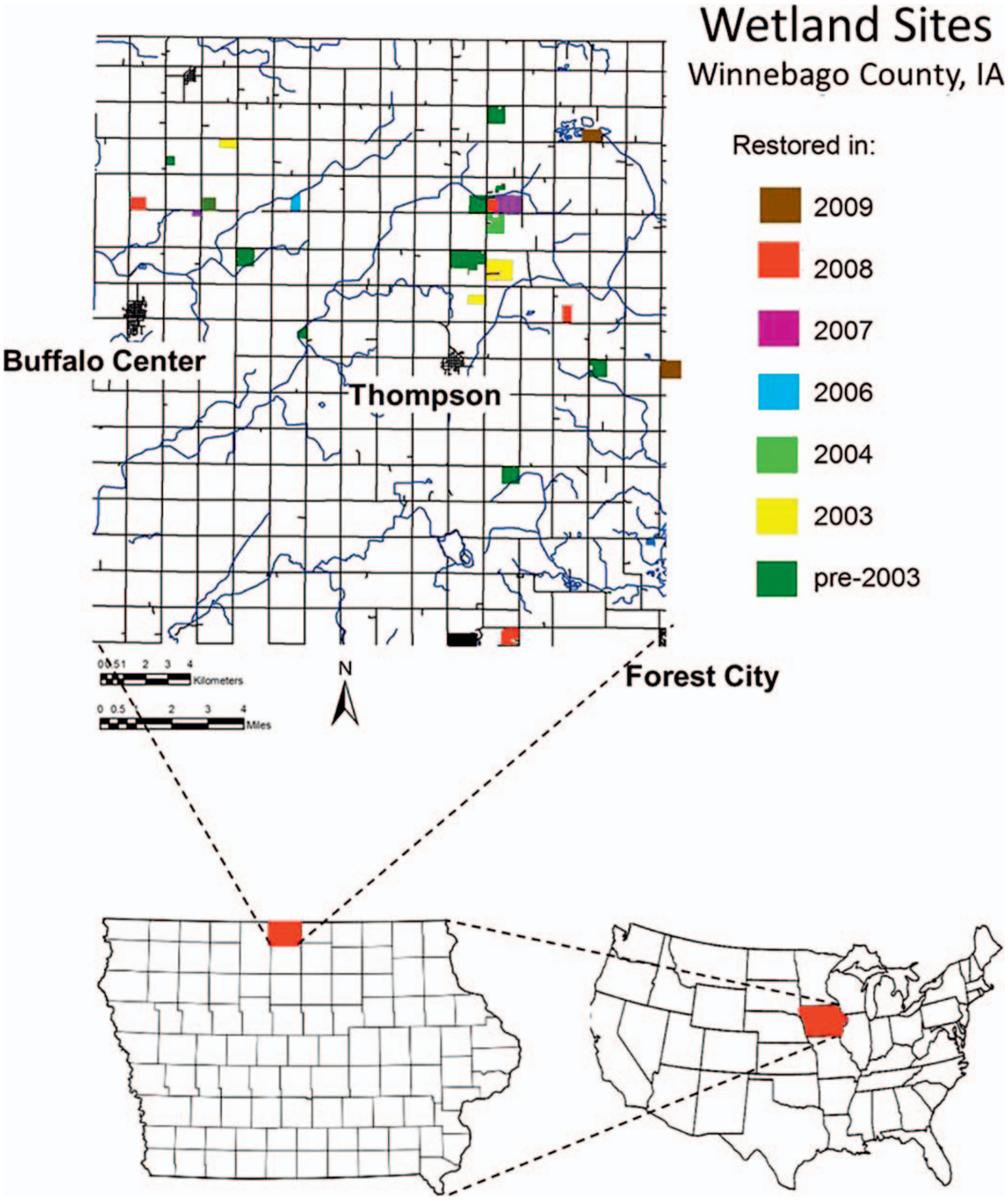

FIG. 1. Winnebago County (red square) lies on the northern border of Iowa, USA. Within this county, we surveyed 22 wetlands that varied in size, shape, juxtaposition with other wetlands, and years since restoration.

of recolonization, used radio-telemetry to map specific pathways followed by individuals across the landscape, and used arrays of biophysical models to measure the physiological cost of habitats available to amphibians.

Study Sites.—Winnebago County lies in extreme north-central Iowa and shares a border with Minnesota (Fig. 1). Its landscape is dominated by row-crop agriculture and confinement facilities for production of hogs and chicken eggs. We selected 22 restoration sites that ranged in size, shape, juxtaposition, and years since restoration. Whereas most sites in this study were restored prior to 2008, four sites were restored during the course of this study. Each site contained 1–5 ephemeral wetlands (breeding ponds; ≤1.5 m deep) surrounded by ≥20 ha of restored tall-grass prairie of mixed native grasses and forbs.

We developed annual land cover maps by classifying the landscape into nine categories: corn, soybeans, prairie, pasture, wetland, streams (either natural or dredged drainage ditches, both lined with grassy banks), farmstead, livestock-facility, or roadside ditches. Almost 90% of this landscape was composed of row-crop fields (mean ± SD percent coverage for corn and soybeans = 50.1 ± 1.6 and 37.5 ± 1.4, respectively). About 0.2% of the landscape was wetlands and 6.1% restored prairie that surrounded these wetlands; 1.9% of the landscape was streams and ~4% split among the remaining four categories.

Study Species.—We focused on three anuran species common in the prairie habitats of Winnebago County: Boreal Chorus Frog (BCF; *Pseudacris maculata*), Northern Leopard Frog (NLF; *Lithobates pipiens*), and American Toad (AT; *Anaxyrus americanus*). These three represent a range in size, vagility, and dependence on water (e.g., *Anaxyrus* toads generally tolerate 40–45% loss of their body weight in water whereas *Lithobates* frogs tolerate only 30–35% loss; Thorson and Svihla, 1943). Wetland drainage combined with over-harvesting beginning in the early 1900s contributed to substantial declines in numbers of NLF in northern Iowa (Lannoo et al., 1994). Results from spring calling surveys conducted in 1991–1994 showed NLF occurred statewide, but surveys conducted in 2006–2012 suggested a decline in NLF populations in other parts of Iowa. As a result, the NLF is listed as a Species of Greatest Conservation Need in Iowa (Iowa DNR, 2015). The same statewide surveys showed BCF and AT to be distributed statewide.

Weather Conditions.—To characterize seasonal weather conditions in our study area, we placed a microweather station (Onset Computer Corporation, Pocasset, MA) at the edge of our study area. We recorded 2-m air temperature and relative humidity for the years we conducted radio-telemetry (2009–2011).

Occupancy.—Using visual and auditory encounter methods (Thoms et al., 1997), two or three people surveyed all sites 11, 7, and 3 times in 2009, 2010, and 2011, respectively. Surveys were conducted between mid-April through June for any evidence (i.e., calling, presence of eggs, tadpoles, or adults) of occupancy. Surveying ≥ 2 times each season allowed us to account for imperfect detection (MacKenzie et al., 2006). We calculated multiseason occupancy estimates (MacKenzie et al. 2003, 2006) with the program MARK (White and Burnham, 1999). We used the formulation $\psi(1)\ \varepsilon(.)\ \delta(.)$, where ψ is the initial occupancy, ε is the probability of extinction, and δ is the probability of colonization (MacKenzie et al. 2003, 2006). Because of a limited number of sites ($n = 22$) and few years ($n = 3$), we kept detection probability constant among years for NLF and AT; for BCF, however, we used time varying detection probability among years.

Movements.—We used radio telemetry to map detailed paths of NLF and AT. Individuals >25 g were fitted with 1.8 g, BD-2 radio-transmitters (Holohil Inc., Carp, Ontario, Canada); this weight ratio (<7%) was below the recommended limit of 10% of body weight (Berteaux et al., 1994). Radios were attached externally (as described by Burow et al., 2012) to individuals immediately after breeding (or midway through the season for some) and followed until fall. The BCF were too small to track and were not included for telemetry. Individuals were relocated every 2–3 d and checked every 7–10 d for skin abrasion from the radio belt. We followed the guidelines for using live amphibians in field research (Beaupre, 2004) and our study design was reviewed by the U.S. Geological Survey.

We recorded coordinates for all locations with an "etrex" (Garmin, Ltd., Schaffhausen, Switzerland) Geographic Positioning System (GPS; Universal Transverse Mercator, ±3 m accuracy, NAD83 datum). We imported, mapped, and analyzed these coordinates using a Geographic Information System (GIS; ArcGIS 9.3; Redlands, California, USA).

Estimating Habitat Costs.—Available habitats offer a range of microenvironmental conditions that can affect amphibian activity and growth (Huey, 1991). Operative temperature (T_e: Bakken, 1992) and evaporative water loss (EWL) are effective measures to characterize daily variations in terrestrial microenvironments used by amphibians and to estimate the physiological costs of available habitats (Bartelt, 2000; Bartelt et al., 2010). To characterize daily variations in the microenvironments, we placed three replicates of physical models (Bartelt and Peterson, 2005) in available cover types of different vegetative structure (dense, e.g., restored prairie; and exposed, e.g., corn and soybean fields). Instead of using the entire physical model (including a strain gage) to estimate rates of EWL, we used paired wet–dry models and temperature differences. Testing and analysis beyond that of Bartelt and Peterson (2005) showed paired wet–dry models to consistently overestimate EWL by 34 ± 4.3% (SD); therefore, we reduced the resulting EWL estimates by this overestimate and generated estimates with less bias.

Habitat Use.—Habitat use by animals may vary by sex and spatial scales (e.g., Bergin, 1992; Klaver, 2001; Bartelt et al., 2004). To capture this variation, we tested patterns of habitat use among male and female NLF and AT at two different spatial scales. At the macrohabitat scale, we mapped all locations of telemetered NLF and AT and calculated the frequencies of land cover types used by these animals. At the microhabitat scale, each time we relocated a telemetered frog or toad, we recorded its location with a GPS unit as well as the vegetation type and microenvironmental conditions (i.e., air temperature and relative humidity) of the terrestrial microsite with a digital psychrometer (Check-It Electronics, Elizabeth, New Jersey, USA). To estimate if NLF and AT were selecting particular microsites or conditions, we recorded similar data at a random polar coordinate within 50 m of each used microsite. All measurements were recorded between sunrise and sunset, when humidity levels were lower and more limiting to anurans.

Statistical Analysis.—For each individual NLF and AT, we used telemetry data to calculate mean daily distance and greatest straight line distance (SLD; distance between release and last location). We tested differences in mean distances traveled (daily and SLDs) for NLF and AT separately with an analysis of variance (ANOVA); we compared movement patterns between NLF and AT with *t*-tests. We used circular statistics (Batschelet, 1981; Zar, 1999) to test for significant linearity and bimodal patterns in movements. Because AT traveled substantial distances (i.e., up to 3 km) from study sites, we were able to test factors affecting distances dispersed by AT with an ANOVA. These calculations were not completed for NLF because few left the wetland prairies during the telemetry period. We used SAS v9.1 (Cary, North Carolina, USA) to perform these tests.

To estimate macrohabitat selection on this relatively simple, homogeneous landscape, we estimated the goodness-of-fit between the habitats selected by anurans and all those available with a chi-square (χ^2) test and then calculated resource selection functions as a proportion of the available resource units on the landscape with a GIS. We used Manly et al. (2002) Design II for our analysis. With Design II, resource use is measured on each individual animal and availability is measured at the population level. To test the null hypothesis that NLF and AT used cover types in proportion to their availability, we then calculated selection indices (w; Manly et al., 2002) using package 'adehabitatHS' (Calenge, 2006) in Program R (R Development Core Team, 2015). Selection for a habitat category was indicated when w differed from 1 and the lower confidence interval was >1. Avoidance of a habitat category was indicated when w differed from 1 and the upper confidence interval was <1. Use of a habitat category in proportion to availability was indicated when the confidence interval for w included 1 (White and Garrott, 1990; Manly et al., 2002). Because of a small number of individually marked animals, we combined all years for our analysis. In reviewing the analysis for the three separate years, we did not find any difference from the combined analysis.

Finally, we tested if telemetered anurans selected microsites that were significantly warmer and more humid than randomly selected microsites. The 22 NLF used upland microsites insufficiently to calculate reliable statistics. For AT, we used a two-stage analysis to account for the toad–toad variation (i.e., random effects) in air temperature (T_a) and relative humidity (RH). Because data were collected by pairing a used and an available site of toad locations (a form of case-controlled data analysis), we used the *clogit* function in the 'survival' package (Therneau and Grambsch, 2000) of Program R to account for the

TABLE 1. Detection probabilities and occupancy rates (±SE) of Boreal Chorus Frogs (BCF), Northern Leopard Frogs (NLF), and American Toads (AT) among restored wetlands in north-central Iowa, USA, 2009–2011, calculated with the program MARK (White and Burnham, 1999).

Species	Year	Detection probability	Occupancy
BCF	2009	0.19 ± 0.05	1.0 ± 0.0
	2010	0.79 ± 0.06	1.0 ± 0.0
	2011	0.91 ± 0.04	1.0 ± 0.0
NLF	2009	0.52 ± 0.06	0.54 ± 0.14
	2010		0.75 ± 0.10
	2011		0.81 ± 0.12
AT	2009	0.51 ± 0.05	0.84 ± 0.12
	2010	0.51 ± 0.05	0.75 ± 0.12
	2011	0.51 ± 0.05	0.78 ± 0.08

pairing of these data. We first fit a logistic regression model of used compared to the random site with both T_a and RH as independent variables for each individual toad (≥10 pairs of observations were required per toad). We then used a random effects meta-analysis with the 'metafor' package (Viechtbauer, 2010) in Program R on the toad-specific estimated slopes to summarize the overall slopes and uncertainty accounting for the toad–toad variation. Unless otherwise noted, we report descriptive statistics as means ± SD; for all tests $\alpha = 0.05$.

RESULTS

Weather Conditions.—Compared to typical conditions for north-central Iowa (www.weather.com/weather/wxclimatology/monthly/graph/USIA0541), weather conditions for this study varied from being cool and wet in 2010 to warm and dry in 2011. Specifically, differences in mean temperatures for 2009, 2010, and 2011 from the 40-yr mean were −0.81, 2.21, and 1.85°C, respectively. For RH, these differences were 8.93, 5.25, and 2.09%, respectively. For precipitation, these differences were 2.59, 14.6, and −9.3 cm, respectively. Hence, conditions for 2009 were closest to mean, though precipitation in the fall was usually high. And although 2011 was generally drier, early spring conditions were sufficiently wet to delay agricultural planting for ~1 mo.

Occupancy.—Occupancy in 2009 for BCF was 1.0 with the probability of both colonization and extinction estimated as 0.0; that is, BCF occupied all sites throughout the study. Probability of detection of BCF increased through time (Table 1). Occupancy (±SE) for NLF was 0.54 ± 0.14, 0.75 ± 0.10, and 0.81 ± 0.12 for 2009, 2010, and 2010, respectively. Occupancy for AT was 0.84 ± 0.12, 0.75 ± 0.12, and 0.78 ± 0.08 for 2009, 2010, and 2011, respectively.

Time for Colonization.—The number of years required for colonization of newly restored wetlands varied by species and distance to the nearest established wetland (Table 2). Boreal Chorus Frogs colonized new wetlands within a year of construction whereas NLF took up to 3 yr to colonize them; AT required up to 2 yr.

TABLE 2. Years required for Boreal Chorus Frogs (BCF), Northern Leopard Frogs (NLF), and American Toads (AT) to colonize newly restored wetlands in Winnebago County, north-central Iowa, USA, 2009–2011.

Site no.	Distance to nearest source wetland (m)	Year restored	Years before first detected: BCF	NLF	AT
22	450	2008	1	1	1
4	1057	2008	1	1[a]	1[a]
19	2845	2009	1	2	2
7	3647	2008	1	3	2[a]

[a] Anurans at these sites were detected after August in these years.

TABLE 3. Number of animals tracked (n), mean weights of animals, duration of telemetry, and mean distances traveled (daily and linear distance moved from the capture location) by telemetered Northern Leopard Frogs (NLF) and American Toads (AT) for each year of the study in Winnebago County, north-central Iowa, USA, 2009–2011. Values for weight, duration, and distances traveled are mean ± SD.

Species	Year	n	Weight (g)	Duration (d)	Mean distances moved (m): Daily	Linear distance
NLF	2009	6	39.8 ± 9.8	52 ± 21	32.6 ± 54.3	323 ± 446
	2010	9	39.7 ± 8.2	22 ± 9	19.2 ± 18.7	123 ± 117
	2011	7	33.3 ± 8.7	22 ± 9	18.1 ± 12.3	131 ± 78
AT	2009	13	36.8 ± 8.4	46 ± 30	56.1 ± 42.7	697 ± 931
	2010	18	35.8 ± 6.9	44 ± 34	72.4 ± 121.7	837 ± 563
	2011	23	38.2 ± 6.9	43 ± 25	33.6 ± 24.6	448 ± 392

Movement Patterns.—We tracked a total of 22 NLF and 54 AT from 2009–2011 (Table 3). The NLF were tracked a mean of 36 ± 22 d and AT a mean of 44 ± 27 d; we tracked 6 NLF >50 d and 10 AT >70 d. Causes for ending telemetry of individuals included predation ($n = 20$), belt escape ($n = 20$), broken belt ($n = 3$), end of battery life ($n = 15$), signal loss ($n = 6$), and 11 died from causes unrelated to telemetry (e.g., dehydration, crushed by agricultural equipment). Overall, there were no differences in mean weight of NLF and AT across the 3 yr (37.4 ± 10.4 g and 36.5 ± 7.2 g, respectively; $F_{3,50} = 1.62$, $P = 0.20$). Individual contrasts showed no difference in the mean weight between male and female NLF (35.3 ± 9.2 g and 42.2 ± 12.1 g, respectively; $t_{20} = 1.39$, $P = 0.09$), but male toads were ~10% lighter than female toads (35.0 ± 6.8 g and 39.1 ± 6.8 g, respectively; $t_{52} = 2.04$, $P = 0.023$).

Mean daily distances traveled by NLF were about half of those traveled by AT (21.7 ± 13.3 m and 50.5 ± 38.6 m, respectively; $t_{73} = 2.919$, $P = 0.002$). Within each species, there were no significant differences in daily distances traveled related to sex ($F_{4,49} = 0.01$, $P = 0.91$), and differences caused by weight of the animal approached significance ($F_{4,49} = 3.97$, $P = 0.052$). There was a large and significant difference in daily distances traveled among the 3 yr of telemetry (Table 3; $F_{4,49} = 10.28$, $P = 0.0002$).

Mean SLDs traveled by NLF were only about one-quarter the SLDs traveled by AT (176 ± 203 m and 698 ± 614 m, respectively; $t_{73} = 3.798$, $P = 0.00015$). The range of SLDs traveled by NLF was 31–857 m while the range for AT was 42–2,932 m; 14 AT traveled >1,000 m and two traveled >2,000 m. Within each species, SLDs traveled varied among years ($F_{4,49} = 2.65$, $P = 0.044$) with the longest distances traveled in 2009 (Table 3). In addition, the number of days an AT was tracked explained about 7% of the variation in SLDs traveled by AT; although this is a small amount, it was statistically significant ($F_{1,53} = 4.29$, $P = 0.043$). Duration of telemetry was not as important a factor in explaining SLDs traveled by NLF ($F_{1,20} = 3.20$, $P = 0.089$). Straight line distances from wetlands for AT were influenced by the relative size and shape of the wetland (Table 4). Smaller wetlands (i.e., <8 ha) required more time for AT to colonize. This measure was not applicable for NLF because they did not leave their study sites.

TABLE 4. Factors affecting straight line distances (rates and patterns of dispersal) by American Toads from restored wetlands. This also reflects the length of time required for American Toads to colonize newly restored wetlands in Winnebago County, north-central Iowa, USA, 2009–2011.

Source	df	Mean square	*F* value	*P*
Sex	1	60.53	0.29	0.5938
Year	2	43.39	0.21	0.6515
Size	1	3869.63	18.41	<0.0001

Only three AT and one NLF traveled in a statistically linear path; all others traveled in random paths (Fig. 2). The number of days tracked or SLD traveled by individuals seemed unrelated to linearity of paths. Specifically, SLDs traveled by AT that followed linear paths were 81, 985, and 1,464 m; these toads were followed 79, 33, and 19 d, respectively. The single NLF that followed a linear path was tracked for 12 d and had an SLD of 87 m.

Physiological Costs of Habitats.—Because postbreeding air temperatures never dropped below freezing until fall (approaching hibernation), we based physiological costs on rates of EWL. Maximum (daytime) rates of EWL approached 50, 40, and 60 g/d in 2009, 2010, and 2011, respectively, reflecting differences in amounts of precipitation during these years. Daily rates of EWL varied according to periods of rain and vegetative structure: they were consistently lowest and least variable in prairie compared to row-crop fields (Fig. 3). Daily rates of EWL dropped substantially in crop fields after corn and soybean plants had grown sufficiently to shade the models and reduce the loss of transpired water; only then did EWL rates reflect those of prairie. Toads moved through row-crop fields when corn and soybeans reduced rates of EWL (usually $\leq$27 g/d); they left these fields when the crops were harvested. An exception to this pattern occurred in 2011 when unusually wet, early spring conditions allowed AT to travel across barren fields before planting. We never followed or observed NLF to travel more than $\sim$15 m into crop fields at any other time of the year. Frogs that left wetlands (and surrounding prairies) generally frequented roadside ditches or grassy banks along streams.

Macrohabitat Selection.—We obtained habitat use for 19 NLF. They demonstrated significant habitat selection ($\chi^2_{152} = 1{,}836$, $P < 0.001$) and identical use of habitats ($\chi^2_{144} = 105$, $P = 0.994$). The NLF strongly selected for wetlands and rarely were found far from wetlands or outside the prairies that surrounded wetlands. They significantly avoided corn and bean types (Table 5) and we

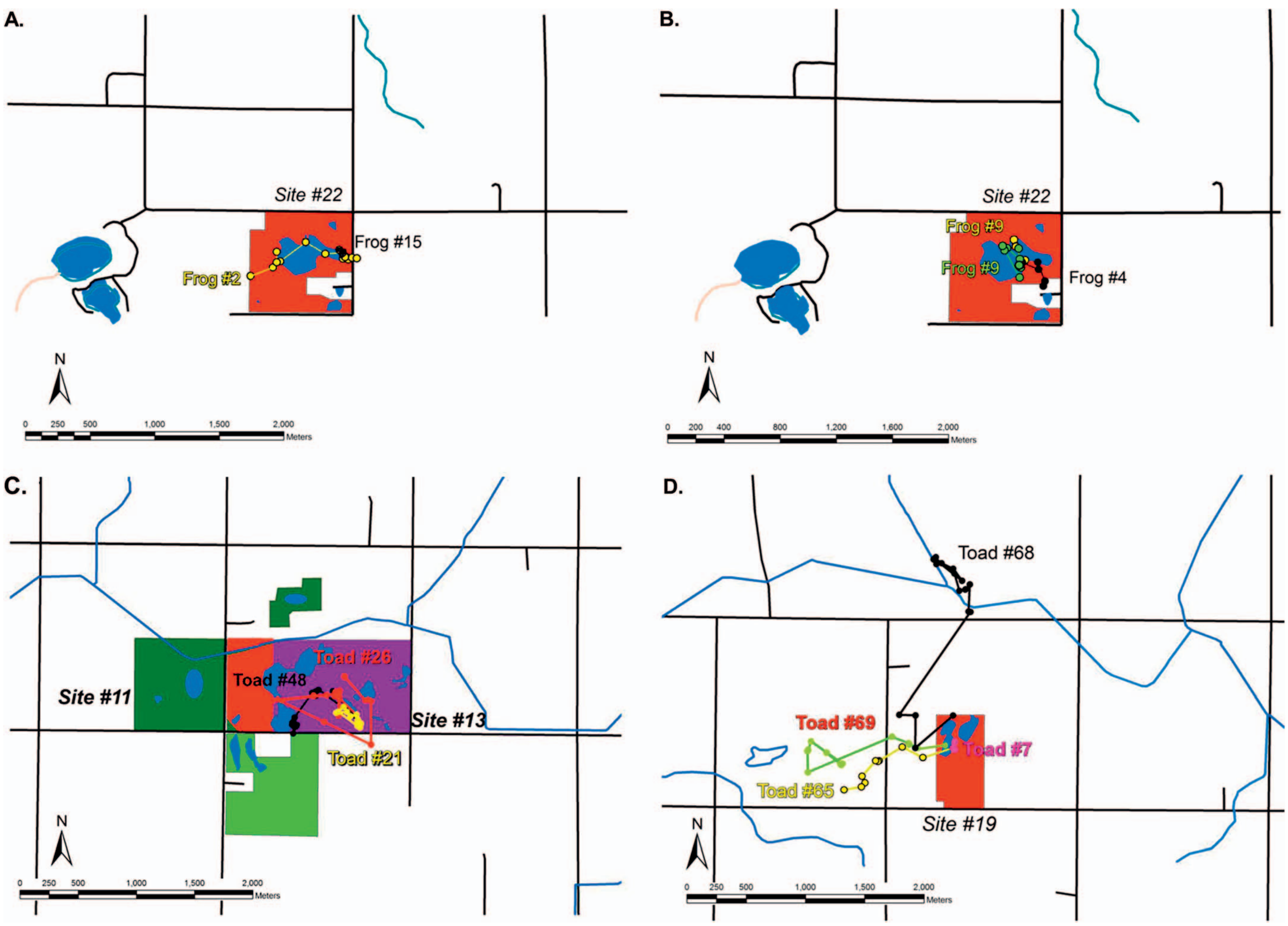

FIG. 2. Examples of movement paths followed by telemetered Northern Leopard Frogs (NLF) during (A) 2010 and (B) 2011, and American Toads (AT) during (C) 2010 and (D) 2011. The NLF rarely left wetland sites except during wet conditions (e.g., 2010). The AT almost always left ponds after breeding; some stayed within the interior of large (e.g., 100 ha) prairies (C); others moved through row-crop fields (D). Colored rectangles = restoration sites (color represents age of restoration; see legend in Fig. 1) surrounded by row-crop fields (white areas). Black grid lines = roads. Blue patches = breeding ponds and blue lines = streams.

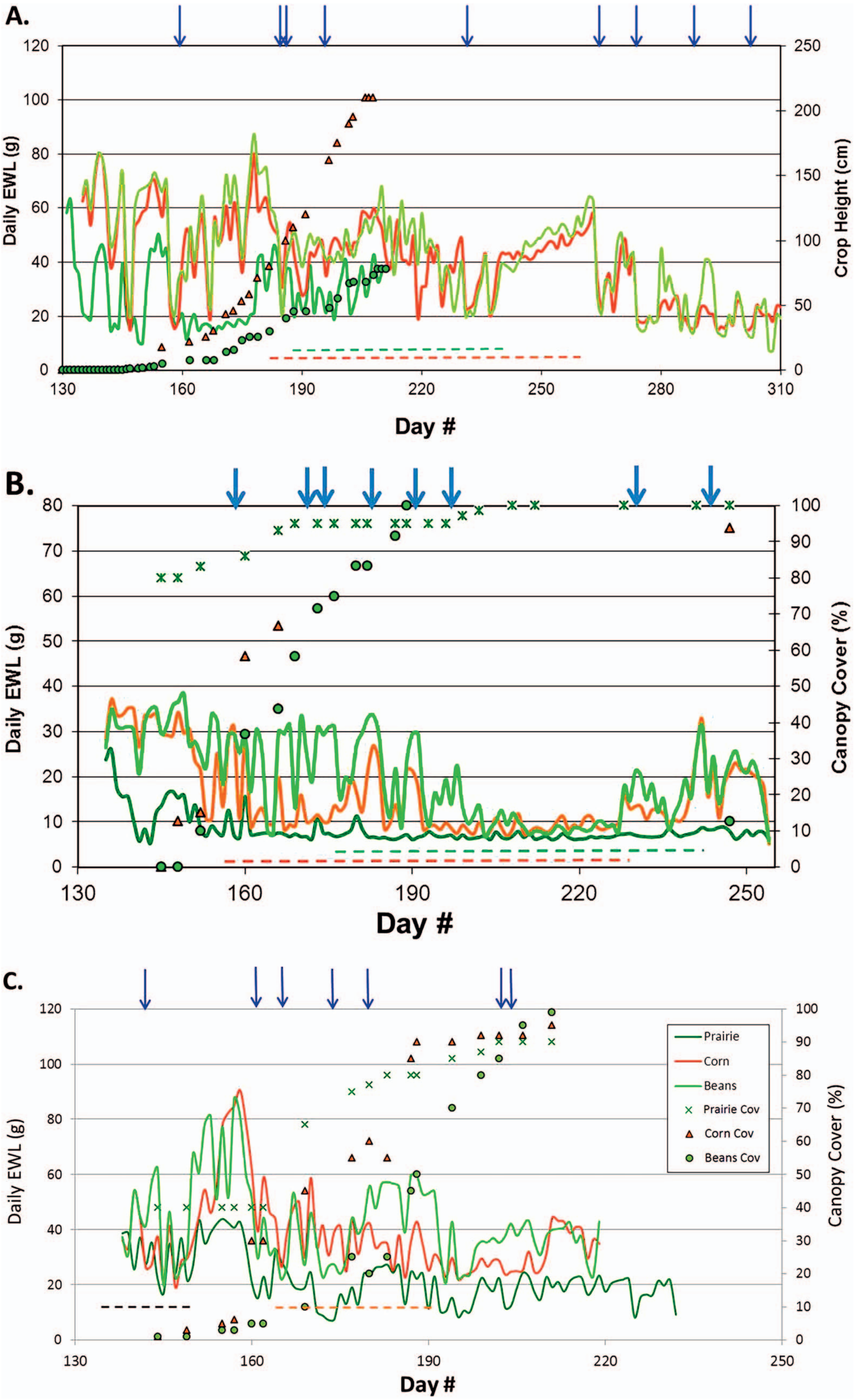

FIG. 3. Physiological costs of habitats in (A) 2009, (B) 2010, and (C) 2011 among habitats in Winnebago County, Iowa, USA. Primary y-axis is rate of evaporative water loss (EWL) and secondary y-axis is growth of vegetation (legend in panel C). Rainfall events of ≥2.54 cm are indicated by blue arrows. The EWL was lowest in prairies throughout the season and diminished for corn and bean fields throughout the season as these crops grew. Use of row-crops by American Toads is indicated by dashed lines near the bottom of each panel, color-coded by crop type (black dashed line = use of barren crop fields during extended spring rains prior to cultivation).

TABLE 5. Estimation of selection indices (w_i) for different macrohabitat types available in Winnebago County, north-central Iowa, USA, for 19 Northern Leopard Frogs (NLF) and 54 American Toads (AT).

						95% Confidence interval	
Species	Habitat type	Available	Used	w_i	SE	Lower	Upper
NLF	Corn	50.10	2.16	0.0432	0.0246	0.0000	0.1114
	Beans	37.54	0.54	0.0144	0.0147	0.0000	0.0551
	Praire	6.05	16.22	2.6793	0.8438	0.3394	5.0191
	Pasture	0.10	0.00	0.0000	0.0000	0.0000	0.0000
	Wetland	0.20	77.30	386.3319	33.4704	293.5210	479.1427
	Stream	1.90	0.00	0.0000	0.0000	0.0000	0.0000
	Farmstead	1.30	0.54	0.4156	0.4003	0.0000	1.5256
	Livestock	0.30	0.00	0.0000	0.0000	0.0000	0.0000
	Ditch	2.50	3.24	1.2968	0.7236	0.0000	3.303
AT	Corn	50.10	16.52	0.3298	0.0766	0.1179	0.5421
	Beans	37.54	5.30	0.1411	0.0464	0.0123	0.2699
	Praire	6.05	40.36	6.6684	0.6444	4.8815	8.4553
	Pasture	0.10	0.00	0.0000	0.0000	0.0000	0.0000
	Wetland	0.20	30.08	150.3636	16.3718	104.9659	195.7612
	Stream	1.90	0.10	0.0557	0.0550	0.0000	0.2082
	Farmstead	1.30	0.85	0.6516	0.4251	0.0000	1.8305
	Livestock	0.30	0.00	0.0000	0.0000	0.0000	0.0000
	Ditch	2.50	6.78	2.7110	0.6267	0.9731	4.4485

did not observe them using pasture, stream, or livestock types. All other types were neither significantly selected nor avoided.

We obtained habitat use for 54 AT. They demonstrated significant habitat selection ($\chi^2_{552} = 5{,}170$, $P < 0.001$) but not identical use of habitats ($\chi^2_{544} = 1{,}303$, $P < 0.001$). In reviewing the results of eigenanalysis (Calenge and Dufour, 2006), this did not appear to be biologically significant. The AT selected for wetland and prairie types and avoided corn, beans, and stream types (Table 5). They selected ditches at the 90% level but neither selected nor avoided them at the 95% level. We never observed AT using pasture or livestock types. Farmstead was used in proportion to its availability.

Microsite Selection.—Testing protocols required a minimum of 10 sites for each AT; hence, we tested for differences in T_a for 28 AT and in RH for 27 AT. Overall, the environmental conditions of microsites selected by AT were similar to randomly selected sites (Fig. 4), though microsites used by AT were significantly warmer ($\beta = 0.1327$, $P = 0.0083$, 95% CI = 0.0341, 0.2313) with little variability among AT (τ^2 [estimate of amount of total heterogeneity] = 0 ± 0.1327 SE). Used sites also were significantly more humid ($\beta = 0.0309$, $P = 0.0309$, 95% CI = 0.0084, 0.534) with little variability ($\tau^2 = 0 \pm 0.0009$ SE).

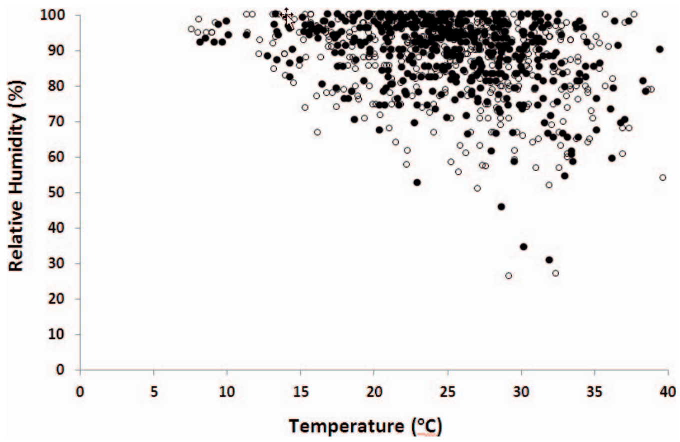

FIG. 4. A comparison of air temperature (T_a) and relative humidity (RH) of sites used by AT to paired randomly selected sites. Ranges of T_a and RH were similar, though sites used by AT were slightly warmer and more humid. Filled circles are used sites; open circles are paired randomly selected sites.

DISCUSSION

After ~20 yr of wetland restorations in Winnebago County, anurans (of at least one species) have colonized all restored wetlands. This study provides evidence of different patterns in occupancy and colonization probabilities by BCF, NLF, and AT.

Occupancy.—By the end of the study, we determined that all three of these species occupied 81–100% of all restored wetlands. We attribute this, in part, to the nature of these wetlands; that is, restored historical wetlands (e.g., Stiles et al., 2016) generally experience greater occupancies than do wetlands created on nonhistoric sites (e.g., Pechmann, 2001).

We observed BCF everywhere and NLF and AT in a majority of wetlands. Habitat differences explained patterns of distribution in other study areas (e.g., McLeod and Gates, 1998; Funk et al., 2005; Peterman and Semlitsch, 2009; Bartelt et al., 2011), and we suspect habitat differences explained why we failed to find NLF and AT at all wetlands here. For example, AT did not occupy wetlands without open, shallow shorelines, so we conclude that differences in habitat features affected patterns of colonization by AT. Except for wetlands ≤3 yr old, we did not observe any patterns of occupancy related to wetland age.

Our study design may have affected detection probabilities for all three species. Specifically, we surveyed for all three species during each visit to the field and began early in the 2009 season to detect the earliest calling. Hence, no calls were heard from some wetlands, causing diminished detection probability. We attribute increasing detection probabilities for BCF from 2009–2011 to improved surveying experience that improved our estimates of detection for these years. Detection probabilities for both NLF and AT were relatively low. The pitch and volume for calls for NLF were low, likely explaining their lower detection probabilities. The AT were late breeding, resulting in few detections until late May, likely causing reduced detection probabilities for these anurans.

Time for Colonization.—Even in wetlands with habitats suitable for all three species, these anurans colonized newly restored wetlands at different rates: BCF always were found in new wetlands the year following restoration while AT and NLF required up to 2 and 3 yr, respectively, depending on the distance from the nearest established site. Time for colonization can be affected by 1) the distance from the nearest source wetland, 2) fidelity to the source wetland, 3) vagility, and 4) characteristics of the intervening terrestrial habitat (MacArthur and Wilson, 1967; Pechmann et al., 2001). We could not estimate the effect of site fidelity to the source wetland in this study, but distances to the nearest source wetlands had a strong and significant effect on time for colonization. Roughly, NLF and AT required 2 yr to colonize restored wetlands >2.5 km from a source wetland and NLF required 3 yr to colonize a restored wetland >3.5 km from a source wetland. We recognize the limited sample size for this conclusion and welcome additional studies to test it; however, the movement patterns and habitat use of NLF and AT, combined with physiological costs of the agricultural matrix, support these conclusions (see below).

Movement Patterns.—AT moved up to 3 km SLD, similar to observations made on this (Bartelt, 1998) and another species of *Anaxyrus* (e.g., Muths, 2003; Bartelt et al., 2004). The NLF moved ≤860 m, less than those at Union Slough (>1 km; Bartelt, 1998) and at another site ~24 km east of this one (>1 km; Swanson, pers. comm.). We cannot explain this difference except that externally attached radio transmitters may have limited movements of NLF in this study.

With four possible exceptions, all telemetered NLF and AT demonstrated random movement patterns; that is, none were statistically linear nor oriented in any dominant direction. This was different from linear-oriented patterns observed in ranids and bufonids in the mountainous forests of the western United States (e.g., Pilliod et al., 2002; Bartelt et al., 2004). We think this reflects a greater homogeneity of the agricultural landscape. Large differences in elevation, together with equally large differences of patchy vegetation in the West (wet or dry grassy meadows, forests of different ages and structure, including clearcuts and talus slopes), created sharp temperature and moisture gradients that shaped anuran movement patterns. Expanses of monoculture, row-crop fields on the glaciated Midwest landscape that vary <100 m in elevation generally lack such gradients.

Physiological Costs.—Among the four cover types tested, rates of EWL were lowest in restored prairie throughout all three seasons. The EWL rates in prairie were highest in the early spring (20–40 g/d) and then began dropping as the new growth emerged. By about early June, rates of EWL were 5–20 g/d and remained low for the rest of the season. Rates of EWL in row-crop fields were high in the spring (approaching 40 g/d in 2010 and 40–60 g/d in 2009 and 2011) and diminished as the crop plants grew in height and cover (usually by mid-June), though they rarely approached the low rates of prairie. We explain this by differences in the density and structure of prairie and crop fields; the dense cover of prairie vegetation best retained water vapor and shaded the ground from solar radiation. Crop plants began retaining water vapor, but only after they exceeded a canopy closure of ~40–60%.

Habitat Selection.—At the microhabitat scale, differences in T_a and RH between microsites used by AT and randomly selected microsites were slight. Some differences among paired sites were simply 1–2°C warmer and had ~2% greater RH, showing an expected preference for warmer, more humid sites. Although these differences were statistically significant, we doubt they are biologically significant. For example, for all anurans in this study, most used microsites had $T_a = 20–35$°C; this is ≥85% of optimal locomotor performance for NLF (Whitehead et al., 1989) and optimal feeding performance for AT (Stevens, 1988). In addition, both used and random microsites had RH = 85–90%. An AT, sitting in a prairie where convection near the ground would be negligible (PEB pers. obs.), would experience only small amounts of water loss. Using the principles of environmental biophysics (Campbell and Norman, 1998), under the conditions measured in this study and ignoring any replenishment of soil water through the animal's pelvic patch, an ~50 g toad would lose <10 g water during 12 h of daylight. This is less than one-half the water loss tolerated by toads (Thorson and Svihla, 1943). Given the high degree of homogeneity among microsites within a habitat patch, the large variation in conditions among macrohabitat patches (Fig. 3) better explains patterns of movement and habitat use.

Clearly, NLF and AT have a strong selection for wetlands and prairies, NLF more so than AT. Like Bartelt (1998, 2000), we observed NLF to occasionally travel ≤15 m into a row-crop field but never into its interior. Swanson (pers. comm.) recently observed NLF using these fields to a greater extent, but substantially less than we observed for AT. Row-crop fields were used extensively by a quarter of the telemetered AT and at least a small proportion by another quarter of the AT. The majority of row-crop use occurred in 2009: these AT had bred in a roadside ditch and, after leaving the wetland, had only row-crops available to them. We can conclude that row-crop fields do not limit AT movement and may provide important dispersal corridors for some adults. Generally, however, we did not observe AT to use row-crop fields until the crop grew sufficiently to reduce physiological costs. Finally, though w for both corn and beans was <1 for AT, AT used corn three times more frequently, reflecting the consistently reduced physiological cost of grown corn compared to beans.

Navigating the Agricultural Landscape.—We argue that these different physiological costs, combined with habitat selection and the physiological attributes of these three anuran species, explain times required to colonize restored wetlands. Because anuran species cannot control their EWL physiologically, they must control it behaviorally (e.g., being most active at night, then carefully selecting and using habitats and retreats during the day). The BCF colonized wetlands the year following restoration; their diminutive size allowed them to utilize small spaces where they could escape the drying sun and either retain or replenish body water. In addition, because BCF are freeze-tolerant (LeClere, 2013), they are not dependent on water to over-winter; instead, they can suspend their movements across the landscape with the onset of winter and then resume them when they thaw the following spring. These reasons explain why BCF seemed to have "seeded" the landscape, ready to take advantage of any new body of water appearing on the landscape.

The AT are well adapted for terrestrial life. In addition to their tolerance to losing large amounts of body water, species of *Anaxyrus* (e.g., AT) have a "pelvic patch" (a rough, textured skin that better disseminates soil water; Lillywhite and Licht, 1974) adapted for absorbing soil moisture, extensive lymphoidal sacs to store water, and small "spades" on the bottom of their feet that give them the ability to burrow into the soil, escaping the drying action of the sun. This burrowing ability also allows AT to overwinter in terrestrial habitats, burrowing below the frost line, as did AT nos. 9 and 10 in this study. These abilities allow AT to travel kilometers across grown row-crop fields, overwintering in a subterranean burrow, to reach distant wetlands.

The NLF took the longest time (up to 3 yr) to find newly restored wetlands. In addition to being less tolerant of EWL, they are too large to utilize small soil crevices (as do BCF), cannot burrow into soil (as do AT), and are dependent on bodies of water for hibernation. So, how do NLF travel across the landscape to colonize other wetlands? In the Midwest, large numbers of NLF are crushed while crossing roads during warm rains (Breckenridge, 1944; Merrell, 1970; Carr and Farhig, 2001). In fall of 2009, we captured large numbers of metamorph NLF using roadside ditches. Observations by Bartelt et al. (1998, 2000) and another, later ancillary study (Bartelt, 2012, 2013) showed that NLF primarily use fence lines and roadside ditches with dense vegetation to move across landscapes. Mazerolle (2004) found that streams and drainage ditches facilitated the movement of Green Frogs (*Lithobates clamitans*) across hostile landscapes, and Mazerolle and Desrochers (2005) observed that agricultural fields disrupted the ability of NLF to reach suitable habitat patches. In this study, because NLF follow roadside ditches, fence lines, and drainage ditches to move across landscapes (rather than cutting across fields), we speculate this explains why they require more time to colonize restored wetlands. Unfortunately, continued removal of Iowa fence rows will eliminate this dispersal habitat.

Anurans and Midwestern Agriculture.—The restoration of thousands of hectares of wetlands on the agricultural landscape in north-central Iowa has greatly benefited many wetland wildlife, including amphibians. For example, occupancy probabilities for NLF and AT among these wetlands are greater than some other regions of the state, and NLF do not appear to be declining in Winnebago County as is the case for other parts of the state (Iowa DNR, 2014). Regardless, row-crop fields dominate the area's land cover and affect anurans in multiple ways, both directly and indirectly. We observed direct effects including modes of mortality: for example, four AT were killed by heavy equipment (e.g., soil packers), two more were killed by mowers, another burned in a trash fire, and two dehydrated when they could not escape the drying conditions of unplanted fields during the onset of warm, dry weather. In these ways, row-crop fields functioned as an "ecological trap" (Battin, 2004; Robertson and Hutto, 2006).

Other effects were indirect and more subtle. The predominant effect observed in this study was the greatly increased rates of EWL in row-crop fields. These rates were substantially higher than rates in prairies for a majority of the active season and prohibitively high for NLF. In addition, 20 (26%) of all telemetered NLF and AT were killed through predation; 15 (75%) of these were captured by predators within prairie habitats, consistent with the patterns of habitat selection by these animals, suggesting that extensive row-crop field may concentrate at least NLF and AT into a small portion of the landscape (i.e., wetlands and prairies), facilitating greater ease of predators to find them.

Not all agriculture in the area is row-crop; some pasture and stream banks are mowed or hayed for livestock. In addition, many roadside ditches are burned or mowed and hayed through the summer. Mowing ditches can kill anurans directly, and the subsequent removal of large amounts of vegetation will substantially increase the cost of anurans moving through ditches. For species like NLF, such greater costs could limit their use of ditches as movement corridors.

Implications for Conservation.—For amphibian populations in regions of destroyed or degraded habitat, restoring quality breeding habitat is a key to reversing their decline; parks, refuges, and other publically protected lands provide such habitats. Another approach is to identify large (e.g., ~1,000 ha), privately owned intact habitat tracts for protection such as Priority Amphibian and Reptile Conservation Areas (PARCAs; http://www.parcplace.org/parcplace/resources/parcas-priority-amphibian-and-reptile-conservation-areas.html). In regions like the agricultural Midwest, such areas are limited in number and/or size or they may be separated by distances greater than the dispersal capabilities typical of these small animals. While we do not suggest the system of small, scattered wetlands in Winnebago County is equivalent to a large PARCA of intact habitat, results from this study suggest that small (e.g., 15–130 ha) areas, closely spaced (e.g., ≤3 km), can provide a network of quality breeding ponds to support metapopulations of anurans (Smith and Green, 2005), especially for rapid colonizers (e.g., BCF, NLF, and AT; Brodman et al., 2006), provided the landscape remains permeable (Ray et al., 2002) and connected. Species with more-limited dispersal abilities (e.g., Blanchard's Cricket Frogs, *Acris crepitans*) may not adapt or colonize as easily. Coordinating with other organizations conserving wetland and prairie habitats (e.g., Important Bird Conservation Areas and Wetland Production Areas) would benefit multiple species including amphibians. Finally, continued climate change that alters the environments of microhabitats may increase the cost of habitats and complicate dispersal rates (Wright, 2010).

Although roads can be important impediments to amphibian movements, we found roadside ditches were an important alternative to row-crops, especially for NLF. Burning or mowing ditches for hay production can harm anurans directly (i.e., killing) and indirectly (i.e., greatly increasing the cost of moving through them). Given the highly degraded state of >95% of the Midwestern landscape, we caution against these practices for a number of conservation reasons, especially for protecting amphibian corridors.

Finally, Semlitsch (1998) proposed a 200-m buffer around breeding wetlands to protect amphibian populations from human activity and Heemeyer et al. (2012) recommended a 1-km buffer to specifically protect Crawfish Frogs (*Lithobates areolatus*). In this study, a prairie buffer of ~200 m seems appropriate. Our results also suggest that size, shape, and location of wetlands within the larger restored site can influence the amount of dispersal of adults from the site, potentially leading to colonization of new sites (at least for AT). For example, in 2009 all telemetered postbreeding adult toads dispersed from a flooded ditch (surrounded by row-crop fields with no prairie buffer) and traveled up to 3 km. In 2011, none of the telemetered postbreeding adults left the 130-ha prairie that surrounded centrally located wetlands. Finally, in 2011, about two-thirds of the telemetered AT dispersed from a narrow 30-ha prairie in which the wetlands occurred at one end within 100 m of neighboring row-crop fields. In this region of the country, where large expanses of intact habitat are rare, designing the size and shape of multiple, small wetlands could help promote the dispersal of adult anurans and establish effective metapopulations on an otherwise unfriendly landscape.

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