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Original article

Home ranges and space use of muskrats *Ondatra zibethicus* in restricted linear habitats

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Modern farming practices in the midwestern United States have drastically altered the landscape. Most wetlands have been drained, and small streams are channelized to transport excess water away from tile-drained agricultural fields. Loss of critical wetland habitat has shifted the distribution of muskrats *Ondatra zibethicus*, an economically important furbearer in the region, to highly altered riparian habitats with unstable flow regimes. However, information regarding home-range size and space use for muskrats occurring in these linear habitats is lacking. We used location data from 26 radio-marked muskrats to estimate home-range size and space use in riparian habitats in an agroecosystem in east-central Illinois, USA. Home ranges were highly linear and confined to stream bank edges. Contrary to our prediction, muskrats did not freely move to upland habitat (e.g. row-crop agriculture) adjacent to stream edges to forage. Linear home ranges were longer for adults than for juveniles. Home-range size also was related positively to number of burrows used by individuals. As expected, muskrats used space non-randomly within linear home ranges with most movements aggregated around established bank burrows. Muskrats in riparian habitat are multiple central-place foragers. Our study provides insight into how muskrats, a semi-aquatic species affected by large-scale landscape change, use space within highly restricted linear habitats.

Key words: home range, linear habitat, muskrat, Ondatra zibethicus, space use, telemetry

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Knowledge of a species' spatial ecology is critical for directing conservation efforts, especially for species that are rare (Schooley & Branch 2006), exploited for harvest (Koen et al. 2007) or occur in highly disturbed, human-dominated habitats (Beasley et al. 2007, Tucker et al. 2008). Estimating home-range size is one common approach for quantifying space requirements for a species (Powell 2000). Home-range sizes can also be used to discern habitat requirements (Mitchell et al. 2002) and direct future management efforts (Lambert et al. 2008). Patterns of space use within home ranges also provide insights into how animal movements are related to habitat heterogeneity (Wauters et al. 1994, Chamberlain et al. 2007).

Increased agricultural production in the midwestern USA has resulted in loss of ~ 98% of the natural wetlands in the region (Suloway & Hubbell 1994). Furthermore, many small headwater streams in the region have been channelized to accept runoff from adjacent tile-drained agricultural fields, thus increasing the variability of their flow regimes (King et al. 2009). These dramatic landscape modifications have affected the distribution of muskrats *Ondatra* *zibethicus*, a species obligately associated with semiaquatic habitats, by restricting most of their suitable habitat to linear small streams and agricultural ditches. Muskrats are an economically important furbearer species in the region. For example, an estimated 439,796 muskrats were harvested in Illinois during 1998-2008, accounting for ~ 25% of all furbearers harvested (i.e. 1,728,208) during that period (Lischka et al. 2010).

Data describing space use by muskrats are limited and mostly apply to individuals occurring in two-dimensional wetland habitats (Errington 1939b, Sather 1958, MacArthur 1978, 1980). For instance, Errington (1939b) reported muskrats range an average of 256 m from the shoreline into the marsh. However, Sather (1958) reported recapturing muskrats 70 m from lodge shelters, whereas MacArthur (1978, 1980) estimated average movement distances of 150-230 m away from lodge or burrow shelters. Again, these coarse estimates of movements were made in two-dimensional wetland habitats. The unique structure of linear habitats can influence the spatial ecology of species (Serena et al. 1998, van der Ree & Bennett 2003, Pattishall & Cundall 2008, Gomez et al. in press), and comparative studies of space use have reported differences in home-range size for species between linear and two-dimensional habitats (Quin 1995, van der Ree & Bennett 2003).

It is unclear to what extent muskrats use upland habitat within their home ranges. Errington (1938, 1941) observed muskrats moving upland to selectively forage on non-native food sources (e.g. corn and apples). However, Dixon (1922) reported that muskrats forage exclusively on vegetation within the stream channel. Published data characterizing space-use patterns of muskrats occurring within linear riparian areas are extremely limited (Brooks 1985), although these areas constitute much of the available habitat for muskrats in the midwestern USA.

Our objectives were to determine the size of home ranges for muskrats in riparian areas, to identify which local habitat and biological factors predict home-range shape and size and to elucidate how muskrats use space within their home ranges. Errington (1938, 1941) reported that muskrats freely move from wetland habitats to forage on row-crop agriculture. We predicted that muskrats in small streams and agricultural ditches would also use upland habitat (e.g. row-crop agriculture) adjacent to streams as well as natural vegetation along stream-bank edges. Because muskrats in two-dimensional habitats are considered central-place foragers (MacArthur et al. 1997), we predicted that muskrats positioned in highly linear stream habitats would also spend most of their time in or near established burrows. We addressed these objectives by tracking movements of radio-marked muskrats within highly linear stream habitats in a human-dominated agroecosystem.

Material and methods

Study area

Champaign County is located in east-central Illinois (40°12'N, 88°26'W) and is embedded in the Grand Prairie region of the USA. Our study area (~ 71,715 ha) is flat and dominated by row-crop agriculture. Due to increased agricultural production and extensive drainage projects, 98% of the county's historical wetlands have been lost (McCauley & Jenkins 2005). Currently, 85% of the landscape is characterized by soybean *Glycine max* (40%) and corn *Zea mays* (45%) production, while historical wetlands cover only 0.9% of the region (Suloway & Hubbell 1994, McCauley & Jenkins 2005). Consequently, agricultural ditches and small streams now provide most of the available habitat for muskrats. The region receives ~ 171 cm of annual precipitation, and has average temperatures ranging from -8.5 to 30.0° C (National Climatic Data Center 2010).

We selected 10 sites positioned within stream segments in three distinct watersheds (Kaskaskia River, Embarrass River and Black Slough). All sites were located within 1st, 2nd and 3rd order stream segments (Strahler 1957), positioned within varying-sized drainage basins ($\bar{x}$ = 63.57 km^2, range: 9.30-141.82 km^2) and stratified by distance away from the headwaters. Average nearest-neighbour distance between sites within each watershed was 5.39 km (range: 1.70-8.15 km). Stream channel geomorphology also varied between sites, with average thalweg depths ranging from 0.23 to 0.55 m and average wetted width ranging from 3.14 to 11.41 m. Reed canary grass *Phalaris arundinacea*, an aggressive non-native species, was the dominant stream bank vegetation at all sites. Broom sedge *Andropogon* spp., big bluestem *Andropogon gerardii*, goldenrod *Solidago* spp., willow *Salix* spp., eastern cottonwood *Populus deltoides* and Indian grass *Sorghastrum nutans* dominated upland riparian vegetation. Muskrats were not harvested by fur trappers at any sites during the duration of our study.

Capture and radio-marking

We live-trapped muskrats using single-door, collapsible traps (Tomahawk Live Trap Inc., Tomahawk, WI; Model 202), and we conducted trapping opportunistically from 6 July to 19 November 2007 and from 14 June 2008 to 29 November 2008 depending upon water levels and minimum temperatures. We fastened live-traps on adjustable trap platforms (2-cm thick plywood of 76 × 25 cm) attached to three stabilizing legs (1.5-cm PVC pipe, 91-cm long; Schooley & Branch 2006) and placed them along stream bank edges near active muskrat burrows or in areas with abundant muskrat signs (e.g. tracks, scat and clippings). Platform height was adjusted daily to compensate for varying water levels. We baited traps with either apple or carrot, opened 1 hour before sunset and then checked 1-2 hours after sunrise the following day.

In 2007, we fitted captured muskrats with 25-g radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota; Model 1565) affixed to a cable-tie collar. The transmitter attachment was completed at the site of capture. Some mortality of muskrats in 2007 may have been indirectly linked to this radio-marking method (i.e. chafing was noted around the neck of some recovered carcasses). Therefore, we used radio-transmitter implants for muskrats in 2008. We transported captured muskrats to a sterile surgical laboratory at the Small Animal Clinic at the University of Illinois College of Veterinary Medicine and pre-medicated individuals with 0.2 mg/kg atropine sulfate to minimize tracheal secretions and 0.5 mg/kg medetomidine for sedation, and then induced surgical anesthesia by facemask using 5% isoflurane and 0.6 L/min oxygen. We surgically implanted a 14-g radio transmitter (Advanced Telemetry Systems, Model M1215) into the peritoneal cavity of each muskrat using standard surgical techniques (MacArthur 1980, Zschille et al. 2008). Post-surgery, each muskrat was administered 0.25 mg/kg atipamazole as a reversal for the medetomidine, 0.2 mg/kg meloxicam as an analgesic and 0.1 ml of penicillin to help minimize the likelihood of post-operative infection. After being held for ≥ 2 hours to monitor recovery, we released muskrats at their point of capture. In both years, we used passive integrated transponder (PIT) tags (Schooley et al. 1993) to mark individual muskrats. All trapping and radio-marking procedures were conducted in accordance with the University of Illinois Institutional Animal Care and Use Committee Protocol # 07105.

Home-range analysis

Most individuals (N = 20) were marked between September and November each year. Individuals were radio-tracked throughout the year; however, most muskrats (77%) were radio-tracked during fall-winter (September-March). Muskrat activity is mostly diurnal or crepuscular during these seasons (MacArthur 1980), so our tracking effort was concentrated during those times (76% = diurnal locations and 24% = crepuscular locations). We determined locations of muskrats ≥ 2 times per week using ground-based telemetry. We used a 3-element Yagi antenna and receiver (Advanced Telemetry Systems, Model R410) to find the general location of muskrats. Based on the transmitter signal strength, we could determine if muskrats were inside or outside of a ground burrow. If an individual was in a ground burrow, we determined the exact location by removing the Yagi antenna and using the receiver and antenna cord to locate the strongest signal along the bank. If muskrats were found foraging in the open, we cautiously approached the individual and recorded the exact location at which the animal was encountered. Although most active encounters did not appear to affect muskrat movements, we acknowledge a potential bias in this method. We recorded all locations using a hand-held GPS unit (Garmin International Systems, Olathe, Kansas; Model GPS 76) with Wide Area Augmentation System (WAAS) capabilities that provided 2-3 m accuracy.

In our study area, muskrat habitat was confined to narrow, linear stream channels surrounded by row-crop agriculture. Commonly used home-range estimators (e.g. minimum convex polygons and kernel density estimators) can overestimate the home-range sizes (Blundell et al. 2001, Downs & Horner 2008) and may underestimate the travel distances in these linear habitats (Knight et al. 2009). Furthermore, kernel density estimators can substantially overestimate the amount of 'used' area when there are multiple relocations at a single place (Seaman & Powell 1996, Pattishall & Cundall 2008) such as a burrow. Measuring the linear or meandering length of habitat within the extent of an individual's known movements has provided accurate home-range estimates for individuals within restrictive habitats (Serena et al. 1998, van der Ree & Bennett 2003, Melero et al. 2008, Pattishall & Cundall 2008). We estimated linear home ranges (LHR) for individual muskrats by measuring the total meandering stream channel length between the most upstream point and the most downstream point using linear measuring tools in ArcMap 9.2 and maps obtained from digital orthophoto quadrangles (DOQs). None of the home ranges included branching within the stream system and were assumed to be from post-dispersal muskrats.

Methods for estimating sample size requirements for LHRs are not well developed. We estimated the minimum number of locations necessary by bootstrapping area-observation curves (Animal Movement Extension to ArcView 3.3; Environmental Systems Research Inc. 2006) using 100% minimum convex polygons (MCP). We fit area-observation curves for a subset of muskrats ($N = 17$) that occurred in straight streams (MCP performs poorly for more sinuous streams) using bootstrapping with 100 iterations and sampling with replacement. For these individuals, LHR was correlated with MCP ($r = 0.92$, $P < 0.0001$). Generally, 20 locations were adequate to estimate home ranges based upon the asymptotes of individual area-observation curves. Based on this criterion, 16 muskrats had sufficient sample sizes and another 10 were borderline (≥ 15 locations). We used all 26 individuals in our analysis, but checked whether our inferences were robust to sample size (see section Results).

We constructed a set of candidate models *a priori* to determine effects of covariates on LHRs of muskrats. We used general linear models (PROC GENMOD; SAS Institute Inc. 2009) to model our response variable, LHR, as a function of selected covariates. Each competing model included an intercept term, error term and ≤ 3 covariates. We limited the number of estimable parameters in each model to ≤ 5 to avoid over-parameterizing our data while still optimizing model likelihood (Burnham & Anderson 2002). We evaluated competing models using an information-theoretic approach with ΔAIC_c values of ≤ 2 indicating models with substantial support (Burnham & Anderson 2002).

Covariates included number of burrows (burrows), age class (age class), vegetation (vegetation), coefficient of variation for water level (CV), number of locations (locations), wetted width of stream (wetted width), width of the riparian zone (riparian) and the year when animals were radio-marked (year). We determined the number of burrows by each muskrat using radio-telemetry. Age class (juvenile or adult) was determined by weight at capture, which was effective because trapping was conducted during summer-fall when weight differences between young-of-the-year and adults were clear (Errington 1939a). We could not determine the sex of live juvenile muskrats with complete certainty (Dozier 1942), so we did not include the sex of muskrats in our analysis. We measured the percent covered by vegetation (channel vegetation, bank vegetation and flood plain vegetation) for every 50 m within each muskrat's home range, and then averaged the result to obtain a single mean value per LHR. These vegetation cover variables were highly correlated ($r \geq 0.60$, $P < 0.001$), so we combined them using a Principal Components Analysis (PCA; SAS Institute Inc. 2009) into a single variable (vegetation) based on Principal Component one, which explained 73% of the total variance. Instability of the hydrologic regime can affect survival of muskrats (Kinler et al. 1990) and alter movement patterns of small mammals inhabiting riparian areas (Andersen et al. 2000). We quantified hydrologic stability within home ranges of muskrats by calculating the coefficient of variation of water-level change from baseline flow at each site. We measured water levels ≥ 1 time/week from a bridge nearest each muskrat home range ($\bar{x} = 0.26$ km; range: 0.00-1.18 km) with a Sonin® ultra-sonic measuring device. The wetted width of the stream and width of the riparian zone (area of vegetation between the edge of the stream and the adjacent row-crop fields) were measured every 50 m within each muskrat's home range and then averaged. The 'year' variable represented potential differences in unmeasured environmental conditions between years (2007 and 2008) and effects of radio-marking method.

Space use

We used a Morisita Index (I_M; Morisita 1962) to investigate space use within home ranges of riparian muskrats. I_M is an index of dispersion that represents the degree of aggregation within a defined study extent, and is independent of sample size (Hurlbert 1990). A random dispersion pattern is represented by values of $I_M < 1$, with aggregated patterns of dispersion indicated by $I_M > 1$. We calculated the degree of aggregation by dividing stream segments within each animal's LHR into 10-m 'bins' using measuring tools in ArcMap 9.2 and

DOQs. We counted relocation points of each muskrat in each bin and then calculated an I_M value for each individual (Krebs 1999:216) as

$$I_M = N\left(\frac{\sum x_i^2 - \sum x_i}{(\sum x_i)^2 - \sum x_i}\right)$$

where N = number of 10-m bins in an individuals home range, and Σx_i = sum of all bin counts for individual i. We compared differences in I_M values between adult and juvenile muskrats using a Mann-Whitney test (SAS Institute Inc. 2009) with a cut-off value of $P \leq 0.05$.

Results

We used 26 radio-marked muskrats (six collared in 2007 and 20 implanted in 2008) to analyze movements and space use within small streams and agricultural ditches. Individual muskrats were relocated an average of 39 times (SE = 5.35, range: 15-104), for a total of 1,025 relocations. Muskrats were never located > 3 m away from the water's edge (Fig. 1), indicating that individuals in our study area did not generally use upland habitat or the surrounding agriculture for foraging.

Our best approximating model indicated that the length of muskrat LHRs was influenced by age class and the number of burrows used (Table 1; R^2 = 0.53). Adult muskrats had longer LHRs ($\bar{x}$ = 804 m, SE = 171, N = 5) than did juveniles ($\bar{x}$ = 529 m, SE = 53, N = 21). Average LHR of combined age classes was 582 m (SE = 56). Muskrats used an average of 6.54 burrows (range: 3-13), and the length of LHRs was related positively to number of burrows used

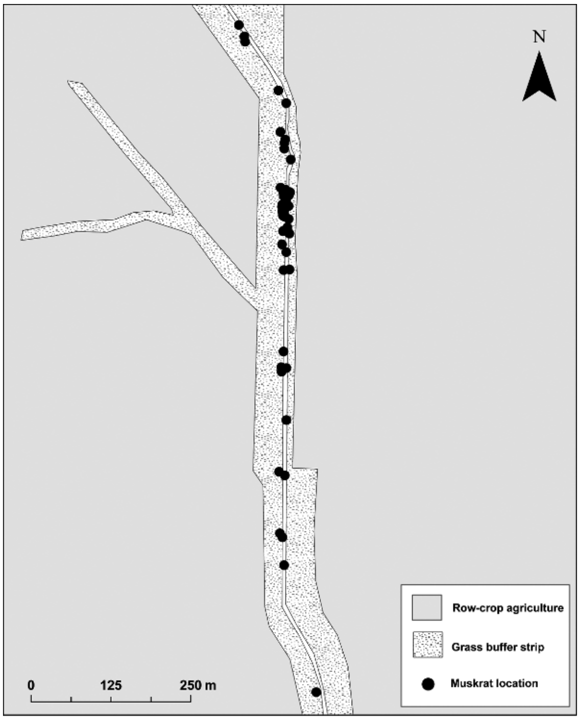

Figure 1. Locations for a radio-marked subadult muskrat from the Black Slough watershed in east-central Illinois, USA, during 27 September 2008 - 28 February 2009. This stream segment had a narrow, grassy riparian zone that was adjacent to row-crop agriculture.

Table 1. Ranking of models predicting linear home-range (LHR) size of radio-marked muskrats within small streams in an agricultural landscape. Models are ranked by ascending ΔAIC_c; K is number of parameters in the model including the intercept and error term; ω_i is the model weight and Log likelihood is used for assessing goodness of fit. Independent variables include burrows (number of burrows within an individual's home range), age class (Adult or Juvenile), vegetation (Vegetation PCA coefficients), CV (coefficient of variation in water levels), year (2007 or 2008), wetted width (wetted width of the stream), locations (number of relocations per individual) and riparian (riparian width).

Model	K	ΔAIC_c	ω_i	Log likelihood
LHR (burrows + age class)	4	0.00	0.71	-173.72
LHR (burrows + age class + year)	5	1.91	0.28	-173.13
LHR (burrows)	3	9.02	0.01	-179.64
LHR (burrows + vegetation)	4	11.15	0.00	-179.29
LHR (age class)	3	12.82	0.00	-181.54
LHR (.)	2	14.39	0.00	-183.61
LHR (CV)	3	14.39	0.00	-183.61
LHR (locations)	3	14.45	0.00	-182.35
LHR (age class + year)	4	14.96	0.00	-181.20
LHR (year)	3	15.36	0.00	-182.81
LHR (wetted width)	3	16.45	0.00	-183.36
LHR (riparian)	3	16.72	0.00	-183.49

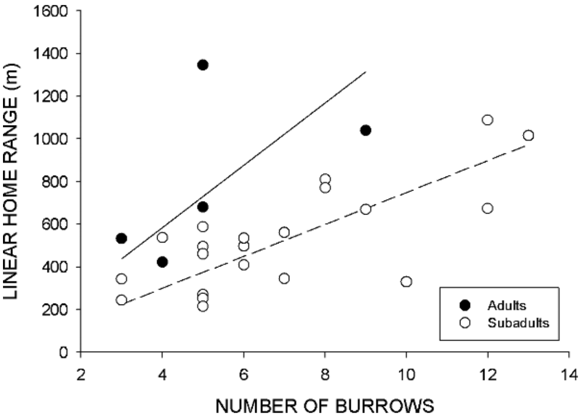

Figure 2. Relationship between home-range size and number of burrows for adult and subadult riparian muskrats within small streams in an agricultural landscape. Each circle represents an individual muskrat (N = 26).

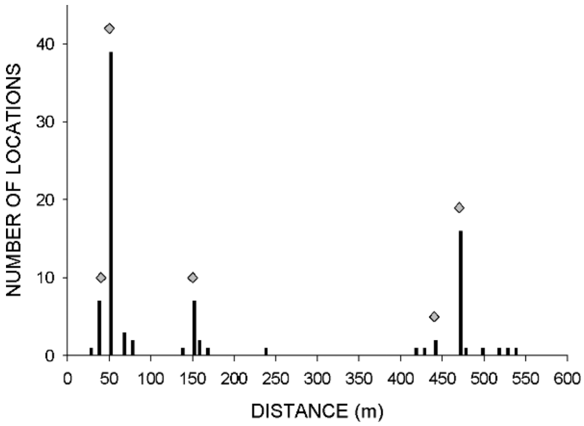

Figure 3. Utilization distribution representing space use within the linear home range (LHR) of an adult muskrat within a small headwater stream. Diamonds represent locations of established burrows within the LHR. Space use was aggregated around established burrows.

(Fig. 2). Our only other competing model ($\Delta AIC_c <$ 2) also included the variable 'year' (see Table 1). However, the addition of 'year' to our most supported model did little to improve model fit (see Table 1), indicating that this additional parameter was not informative (Anderson 2008). A similar analysis using only muskrats with ≥ 20 locations (N = 16) also indicated that LHRs were related to age class and number of burrows; the only two models with substantial support included these two predictors.

Mean I_M values indicated that space use by muskrats was highly aggregated ($\bar{x} = 10.92$, SE = 1.50, N = 26). Adult muskrats had higher I_M values ($\bar{x} = 19.87$, SE = 2.24, N = 5) than did juveniles ($\bar{x} = 8.79$, SE = 1.37, N = 21; z = 2.862, P = 0.004). The frequency of locations as a function of linear distance along the LHRs suggested that space use was aggregated around established burrows (see Fig. 3 for a representative example).

Discussion

Our results provide a clear example of how muskrats, a species affected by large-scale landscape change, use space within restrictive linear habitats. Home ranges of muskrats were highly linear and confined to the contour of stream bank edges. Contrary to our prediction, muskrats did not freely move upland and into adjacent row-crop agricultural fields to forage. This pattern suggests that available vegetation along the stream edge, which was primarily reed canary grass, provided sufficient forage. Muskrats used space non-randomly within LHRs with most movements occurring near established burrows (see Fig 3). These results are consistent with other studies in wetlands (MacArthur 1978, MacArthur et al. 1997) and support our hypothesis that burrow-dwelling muskrats occurring in small streams and agricultural ditches also should be considered as multiple central-place foragers.

Muskrats occurring in restrictive riparian habitats had highly linear home ranges, and the shape of their LHRs largely depended upon the sinuosity of the stream segment (see Fig 1). However, our original prediction that muskrats inhabiting small streams and agricultural ditches would use upland habitat (e.g. row-crop agriculture) adjacent to stream edges was not supported. Errington (1938, 1941) reported that muskrats living in drainage ditches in Iowa, USA, foraged extensively on corn in adjacent fields and transported the corn stalks back to their feeding platforms. In our study area, we did not detect muskrats foraging on corn (i.e. transported stalks, damage to agricultural fields or actual observations) even though it was growing ≤ 6 m from the stream edge in some instances. Reed canary grass is a ubiquitous non-native grass associated with variable flooding regimes (Kercher & Zedler 2004) and most wetlands in Illinois (Matthews & Endress 2008). Reed canary grass was also the dominant bank vegetation at all of our sites, and we observed muskrats extensively foraging on reed canary grass (i.e. visual observations, cached in burrows and on feeding platforms). A concurrent study in our region demonstrated that site occupancy by riparian muskrats during summer-fall was unaffected by dominance of invasive reed canary grass (Bucci 2009). Although the nutritional value of reed canary grass to native herbivores is unclear, the species has been linked with high abundances of some small mammals (e.g. *Microtus* spp. and *Blarina brevicauda*) in the region (Spyreas et al. 2010). Reed canary grass in highly altered riparian habitats could provide enough suitable vegetation so that muskrats do not have to forage far from the stream edge. However, further investigations are needed to clarify the influence of reed canary grass on muskrats occurring in these riparian habitats, especially in winter when reed canary grass is dormant.

Adult muskrats had longer LHRs than did juveniles, and LHRs of riparian muskrats were related positively to number of burrows used per individual. It is unclear why juveniles had smaller home ranges than did adults. In wetland habitats, intraspecific aggression within muskrat populations is intensified as older juveniles move into new territories (Errington 1939b). Hence, intraspecific aggression in restricted riparian habitats could limit the space available to smaller individuals, thus constricting their home range. MacArthur (1980) reported shorter movement distances away from the dwelling lodge during winter (150 m) than in summer (230 m). However, because of our moderate sample sizes, we were unable to examine seasonal variation in muskrat LHRs. Our estimate of the mean number of burrows used per muskrat ($\sim$ 7) is $>$ 3 times greater than that reported by Brooks (1985). Among other reasons, muskrats use burrows for protection from predators (Messier & Virgil 1992). In our region, highly linear strips of riparian habitat are exploited by several species that could prey on muskrats (e.g. coyote *Canis latrans*, red fox *Vulpes vulpes* and American mink *Neovison vison*; Gosselink et al. 2003, Bluett et al. 2006). However, American mink are perhaps the most important muskrat predator in our system especially during winter (Ahlers et al. 2010). Muskrats may be multiple central-place foragers that restrict most of their movements to areas near established burrows in part to remain close to refugia while foraging to reduce predation risk. Thus, individuals with longer home ranges would require more burrows to reduce risk of predation while exploiting resources in different parts of their home range.

Designing and implementing management and conservation efforts for a target species requires an understanding of how landscape structure influences space-use patterns (Chapin et al. 1998). Agricultural production in the midwestern USA has drastically altered the landscape, resulting in the creation of unnatural, linear strips of riparian habitat that represent most of the available habitat for semi-aquatic organisms in the region. Muskrats occurring in these linear habitats restrict much of their movements to stream bank edges, essentially occupying a one-dimensional home range. Future research should be directed towards elucidating how the linear structure of these habitats influences dispersal and gene flow in these highly altered agroecosystems.

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