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Laken S. Ganoe

Matthew J. Lovallo

Justin D. Brown

W. David Walter

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Laken S. Ganoe[1,*], Matthew J. Lovallo[2], Justin D. Brown[3], and W. David Walter[4]

Abstract - Evidence indicating a decline in *Ondatra zibethicus* (Muskrat) populations in the United States during the past 40 years has led to speculation regarding factors influencing Muskrat survival. In order to understand population dynamics and survival, it is important to first define the ecology of local populations. We investigated the dwelling structure use, movements, home range, and survival of radio-tagged Muskrats ($n = 14$) in an urban wetland complex in central Pennsylvania. We used locations collected from intensive radio-telemetry monitoring to determine number of lodging structures used, hourly movement, and size and percent area overlap of home ranges. Muskrats shared an average of 9 lodging structures, and on average, 68% of a Muskrat's home range overlapped home ranges of other Muskrats. We used 4 home-range estimators (kernel density estimator [KDE]$_{href}$, KDE$_{ad\,hoc}$, KDE$_{plug-in}$, and local convex hull estimator) to assess the ability of each estimator to represent Muskrat home ranges. The KDE$_{plug-in}$ that constrained the estimate of home range to habitat boundaries provided the most appropriate home-range size for Muskrats in a linear–non-linear habitat matrix. We also calculated overwinter survival estimates using known-fate models. Our top model indicated a positive effect of the average weekly precipitation on survival, with an overwinter survival estimate of 0.59 (SE = 0.16). The main cause of Muskrat mortality was predation by *Neovison vison* (American Mink; $n = 6$). The small sample size and uncertainty surrounding our model selection led to weak estimates of survival; however, our model suggests that snowfall may be an important factor in Muskrat survival. Our study provides novel data on Muskrat ecology in Pennsylvania as well as preliminary evidence for future investigations of factors affecting Muskrat survival during the winter months.

Introduction

Harvest estimates of *Ondatra zibethicus* (L.) (Muskrat) have declined across the United States since the 1970s, suggesting widespread Muskrat population decline (Ahlers and Heske 2017, Roberts and Crimmins 2010). Several factors may influence Muskrat populations and survival, including predation, habitat loss and degradation, disease, or a combination of stressors (Ahlers and Heske 2017). As a semi-aquatic furbearer, movement and distribution of individual Muskrats on the landscape is centered around water bodies within areas occupied by Muskrat

[1]Pennsylvania Cooperative Fish and Wildlife Research Unit, Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA 16802. [2]Bureau of Wildlife Management, Pennsylvania Game Commission, Harrisburg, PA 17110. [3]Department of Veterinary and Biomedical Sciences, The Pennsylvania State University, University Park, PA 16802. [4]US Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, University Park, PA 16802. [*]Corresponding author - lsganoe11@gmail.com.

populations. With respect to group sizes, Muskrats are semi-colonial and will share their dwelling structures (i.e., huts and bank burrows) with several related and unrelated Muskrats (Ching and Chih-tanc 1962). Muskrats in China were documented sharing 75% of the area of their home range with other nonfamilial Muskrats (Ching and Chih-tanc 1962). In large marshes, Muskrat families may use an average of 1–4 huts (Proulx and Gilbert 1983). This close spatial proximity of Muskrats can result in density-dependent predation or in the direct transmission of disease agents between individuals sharing the same dwelling structures, in turn influencing local population health and Muskrat persistence (McCallum et al. 2001).

Along with understanding the magnitude of dwelling-structure sharing, patterns of space use may also influence Muskrat survival. Space use of semiaquatic mammals is constrained by habitat geometry (e.g., water boundaries) and connectivity. Landscapes with high connectivity or narrow movement corridors may increase the probability of individual interaction and direct disease transmission (Collinge and Ray 2006). Concomitant with the diversity of habitats in which Muskrats reside (e.g., urban wetland complexes, coastal wetlands, river systems, etc.), methods for estimation of home range-size vary between studies, making it difficult to compare space use among studies. For instance, in mark–recapture studies, Muskrats were estimated to have stayed within 70 and 265 m of both huts and shoreline, respectively (Errington 1939, Errington and Errington 1937, Sather 1958). In radio-telemetry studies, estimated home-range size varied from 150–230 m radial distance from huts in a marsh to 800 m along a linear stream habitat where Muskrats used multiple bank burrows (Ahlers et al. 2010a, MacArthur 1980). Muskrat home ranges contain their dwelling structures, and the shape of home ranges varies depending on the habitat type. Muskrats in ponds and marshes tend to have unique two-dimensional summer home ranges from 7 to 85 m in diameter, while those in linear habitats, such as rivers and streams, have home ranges of linear lengths varying from 46 to 800 m (Ahlers et al. 2010a, Erb and Perry 2003). With such variation in landscapes occupied by Muskrats, configuration and size of Muskrat home ranges can be used to understand overlap of individuals and to assess potential contact networks of Muskrats when attempting to determine how space use may impact survival.

Movements of mammals living in aquatic landscapes are also affected by fluctuating water levels, and movements in response to flooding have the potential to affect survival (Ahlers et al. 2010b, Anderson et al. 2000, Naiman and Rogers 1997). Flood events can lead to the displacement of Muskrats for up to 80 hours when their dwelling structures become inundated (Ahlers et al. 2010b). During high-intensity rain events, flood-induced dispersal of Muskrats was expected to increase predation mortality during a study in Illinois, but most of the predation events observed were during non-flood events (Ahlers et al. 2010b). Errington (1954) concluded that in areas experiencing drought, Muskrats have a severe disadvantage and become exposed to *Neovison vison* (Schreber) (American Mink, hereafter Mink) predation that may result in rapid local population declines. Drought exposure during the early winter also results in mink predation events; however, they are infrequent (Errington 1954).

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Although Mink are responsible for most predation events, Muskrats are vulnerable to numerous other predators, with *Procyon lotor* (L.) (Raccoon), raptors, and other mesocarnivores notably contributing to Muskrat mortality (Erb and Perry 2003). In northern North America, Mink predation on Muskrats may be greater in areas where prey diversity is low (Erb et al. 2001, Shier and Boyce 2009, Sunderam et al. 2013). Predation is one of the major causes of Muskrat mortality (Erb and Perry 2003). However, survival is also influenced by a combination of factors including habitat quality, climatic factors (e.g., flooding, drought), disease dynamics, and food availability (Ahlers and Heske 2017, Ahlers et al. 2010b, Ferrigno 1966 Greenhorn et al. 2017).

In addition to drought exposure and predation having variable influences on Muskrat survival rates, there is also variation in survival rates between Muskrat age classes and habitat types. Juvenile survival is lowest from birth to 6 weeks of age and during winter (Stewart and Bider 1974). Juvenile survival rates are extremely variable across study sites and habitats, making it difficult to generalize across the range of the species. Most survival estimates are based on ratios of juvenile to adult females collected from placental counts in harvested females, which can positively bias survival estimates (Erb and Perry 2003). Juvenile survival estimates have varied from 10% to 87% (mean = 44%) between birth and fall, and from 4% to 58% (mean = 17%) annually (Erb and Perry 2003). Adult survival rates also vary widely in space and time. Annual adult survival estimates have varied from 4% to 17% (Clark and Kroeker 1993, Simpson and Boutin 1993). Survival estimates are often even lower in both age classes during the winter months, but little evidence of the causative factors for this difference exist and warrants further study (Erb and Perry 2003).

Regionally, most studies of Muskrat space use and survival have been conducted in the midwestern US and Canada (Ahlers et al. 2010a, Errington 1939, MacArthur 1980), and little information exists for Muskrats residing in the eastern US. The purpose of this investigation was to aid in understanding the ecology and space use of individual Muskrats within a region lacking historic data. Our objectives were to (1) provide understanding of use of dwelling structures, spatial distribution, and hourly movements of a local population of Muskrats during fall and winter, (2) define possible ecological traits that may be contributing to population declines and potential disease transmission within localized Muskrat populations, and (3) determine factors affecting Muskrat overwinter survival.

Field-Site Description

Survey sites were located in an urban complex of ponds straddling a stream in central Pennsylvania (UTM Zone 18T, Datum NAD83, 340606E, 4536363N; Fig. 1). The stream within the wetland complex is ~20 m wide and connects to the West Branch of the Susquehanna River, 1.5 km east of the complex. The depth in the ponds varied from 0.15 m to 1.5 m, and the distance from ponds to the stream was 2 m on average. Total available pond habitat was 1.35 ha and was situated

beside a recreational community park and a shopping center with areas of high human traffic. The mean annual precipitation at the site during 2018 was 157.35 cm, mean annual temperature was 10.1 °C, and.the number of days per year with temperatures below 0 °C was 29 days (NOAA 2014).

Methods

Capture and tagging

We captured Muskrats throughout the study area June–November 2018 using un-baited, double-door, collapsible Tomahawk model 203 live traps (Tomahawk Live Trap Co., Tomahawk, WI) placed on the bank and in grass trails made by Muskrats. Captured Muskrats were moved from the traps into squeeze cages and weighed. We released immediately at the site of capture all Muskrats weighing less than 600 g in adherence to tag and body weight ratios given in the guidelines provided by the American Society of Mammalogists (Sikes et al. 2011). We marked all individuals over 600 g using an ear tag imprinted with a unique ID number (Style 1005-1,
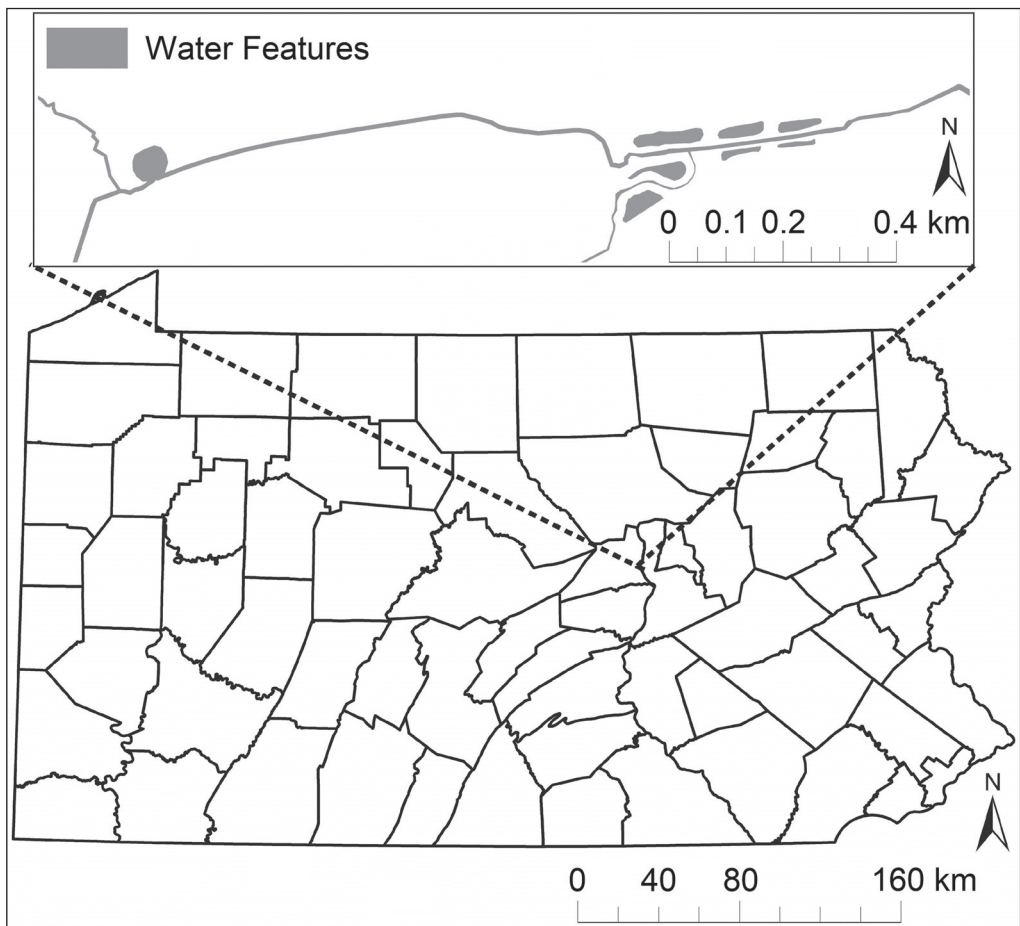

Figure 1. Location of study site in Lewisburg, PA (outset), and the pond-stream matrix where trapping of *Ondatra zibethicus* (Muskrat) occurred during 2018 (inset).

National Band and Tag Co., Newport, KY) and transported them to Metzger Animal Hospital (State College, PA) for implantation of radio-transmitters.

Muskrats were anesthetized by veterinarians using an intra-muscular (IM) injection of Ketamine (10.0 mg/kg) and Medetomidine (0.1 mg/kg). All animals were provided supplemental oxygen by face mask. Level of anesthesia and vital parameters, including muscle relaxation, response to stimulation, relative arterial oxygen saturation (SpO_2), temperature, heart rate, and respiration rate were monitored throughout anesthesia. Each Muskrat had a 13.0-g radio transmitter (model M1215; Advanced Telemetry Systems Inc., Isanti, MN) implanted into the peritoneal cavity following published protocols (Lacki et al. 1989, MacArthur 1980). Post-operative analgesia and antibiotic prophylaxis were provided with Meloxicam (subcutaneous, 0.2 mg/kg) and Penicillin G (IM, 0.1 mL), respectively. We reversed the Medetomidine with Atipamezole (IM, 0.5 mg/kg) and held animals for monitoring a minimum of 2 hours after reversal to ensure complete recovery prior to release at the site of capture. We recorded induction time as the time from administration of the immobilization drug to the animal becoming unconscious and time of surgery as from the initial incision to the final suture. Reversal time refers to the time from the administration of the antagonist to when the Muskrat awakened and was responding relatively normal to stimulation. We report total procedural time as the time from administration of the immobilization drug to the animal awakening and responding to stimulation. We considered young-of-the-year at time of capture to be juveniles, and all Muskrats over 1 year of age to be adults. We based determination of age class on body size and weight with respect to month of capture (Ahlers et al. 2010a, Dorney and Rusch 1953, Proulx and Gilbert 1988). All capture, handling, and surgical methods were approved by the Institutional Animal Care and Use Committee at The Pennsylvania State University (No. PROTO201800187) and are within the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Use of dwelling structures and hourly movement

We monitored Muskrats using a radio-telemetry receiver (model R4000; Advanced Telemetry Systems Inc., Isanti, MN) and 3-element Yagi antennae (Model 13863, Advanced Telemetry Systems) from time of surgery through March 2019. We used homing techniques and visual observation to determine the location of each individual. The distinguishing features at the study site allowed us to effectively mark locations on aerial photographs in the field, which we then digitized in ArcMap 10.5.1 (ESRI 2010) upon return from the field. With limited transmission range (<100 m) requiring observers to track individuals in close proximity, we acknowledge that homing in on Muskrats may have potential observer influences on Muskrat behavior and movements. We recorded >1 location per individual each week for use in survival estimates. We used constant time intervals to limit autocorrelation while maximizing the number of locations collected by observers; however, we do recognize that we are unable to fully account for autocorrelation and bias in our home-range estimation (De Solla et al. 1999, Noonan et al. 2019). We conducted intensive telemetry sessions, where we collected 3 to 6 locations

once per day for each individual, with at least 40 minutes (mean = 52 min, min–max = 40–75 min) between consecutive locations. We conducted a total of 22 days of intensive telemetry sessions spanning the months of September to December. Of locations collected, 60% were diurnal, 31% occurred during twilight, and 9% were nocturnal. We were able to identify the location of Muskrats using radio telemetry and record behavior as either dwelling or non-dwelling, as defined by an individual's presence in or absence from dwelling structures. From these data, we calculated the average number of dwelling structures used per individual by age class. Using intensive telemetry sessions, we calculated the average hourly movement using the mean linear distance between consecutive locations per individual and by age class. We used two-sided *t*-tests to compare means between age classes.

Size of home range

We calculated individual home-range sizes using a local convex hull estimator (LoCoH) and fixed kernel density estimators (KDE) with 3 different smoothing parameters (KDE $_{href}$, KDE $_{plug-in}$, and KDE $_{ad\ hoc}$) in the program R (version 3.5.0) (Bauder et al. 2015, Getz et al. 2007, Walter et al. 2015, Worton 1995). We used different estimators to determine which more appropriately represented Muskrat space use between successive locations for our data based on configuration of home ranges and amount of unsuitable habitat they encompassed. We did not use linear home-range estimators to determine home-range estimates due to the configuration of the study site being a matrix of a linear stream and pond complex (Ahlers et al. 2010a). We restricted analyses to only individuals with >50 locations (*n* = 11) to maximize proper representation of space use by the individual and to potentially minimize influence of repeat locations at dwelling structures. We calculated 50% and 95% isopleths to represent the core and complete home ranges of each individual, respectively. We calculated the average home-range size across all individuals for each isopleth, and then again by age class. Since KDE$_{plug-in}$ best represented the space use of Muskrats, we used the KDE$_{plug-in}$ 95% isopleths and Program R to calculate the percent area overlap of home ranges for all paired combinations of Muskrats. Percent area overlap represents the percentage of an individual Muskrat home range that overlaps another Muskrat's home range.

Survival estimates

We monitored the survival of 14 Muskrats via radio telemetry from release to confirmed mortality, if the individual was still available at the study location. The first 3 Muskrats captured were monitored moving as expected several weeks post-surgery but were predated upon during the summer, weeks prior to the capture of the remaining 14 individuals, and were excluded from the survival analysis. The starting date for known-fate analysis was November when we had 14 telemetry-equipped Muskrats. Four Muskrats died of predation, and we failed to locate 2 individuals in December, 3 in February, and 1 more in March. Only 4 Muskrats were found alive and near the study location at the end of our investigation on 27 March 2019. We determined cause of death by investigating the site and carcass (if available) for signs of predation, including identification of predator species based

on nearby tracks and scat when possible. We calculated weekly overwinter survival rates for Muskrats alive starting 8 November 2018 to 27 March 2019 and included age, average weekly precipitation (AVP), and total degree days (TDD) per week below 0 °C as climate covariates. Age ratios observed in the harvest suggest variation in survival by age class; thus, age was included as a covariate in our models. We used AVP as a covariate in our models to investigate the effect that winter precipitation has on Muskrat survival. We standardized the sum of the TDD indexed around 0 °C because Muskrat movement during the winter months, especially in lentic habitat, is dependent on the presence of ice (Errington 1961). All covariates were standardized to a mean of zero to be able to directly compare model coefficients. We used known-fate models to calculate overwinter survival estimates from individual weekly encounter histories in he program MARK® (version 6.2, Build 9200; White and Burnham 1999). We ranked models using Akaike's information criterion adjusted for sample size (AIC_c) and calculated relative variable importance by summing model weights for each covariate (Burnham and Anderson 2002).

Results

Capture and tagging

We captured 28 Muskrats over 1032 trap nights from 4 June to 16 November 2018. Only 17 Muskrats (7 adults, 10 juveniles; 11 males, 6 females) weighed over 600 g, and were included in this study. There were no complications with surgery, and all physiological parameters monitored were stable throughout anesthesia (see Supplemental File 1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n28-1-N1845-Ganoe-s1, and for BioOne subscibers, at https://dx.doi.org/10.1656/N1805.s1). Surgeries were completed in an average of 18 minutes (min–max = 10–29 minutes), with average induction time of 6 minutes (min–max = 2–33 minutes) and reversal time of 2 minutes (min–max = 2–7 min), resulting in an average procedural time of 38 minutes (min–max = 22–98 minutes). All Muskrats were mobile and behaving normally upon release.

Use of dwelling structures and hourly movement

We collected an average of 81 radio-locations per Muskrat (min–max = 3–162 locations), with 78% of locations at dwelling structures. We failed to detect a difference between the number of dwelling structures used based on age class ($P = 0.50$). The average number of dwelling structures used per individual was 9.17 structures (SD = 2.86). One burrow was used by 8 individuals simultaneously during the autumn months (August–October). The mean distance moved per hour by age class was 27.80 m (min–max = 0.00–300.13 m) for juveniles ($n = 7$), and 27.71 m (min–max = 0.00–306.32 m) for adults ($n = 6$). We did not detect a difference between average distance moved for each age class ($P = 0.98$); therefore, we calculated the pooled mean distance moved per hour during intensive telemetry sessions as a straight linear distance of 27.76 m ($n = 13$, SE = 1.77). During the spring, 1 Muskrat (m16) moved over 750 m upstream from the locations we collected during the fall.

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Size of home range

We calculated home-range size for 11 individuals on which we had over 50 locations each. As expected, the home-range size varied across estimators, with KDE_{href} resulting in the largest home ranges and ones that overestimated the area used by Muskrats in comparison to the actual locations collected. (Table 1, Fig. 2). The LoCoH estimator resulted in the smallest average home-range size and it

Table 1. Total (95%; ha) and core (50%; ha) size of home range for individual *Ondatra zibethicus* (Muskrat) using 4 different estimators: kernel density estimator (KDE) with smoothing determined by reference bandwidth (KDE_{href}), ad hoc reference bandwidth ($KDE_{ad hoc}$), and plug-in ($KDE_{plug-in}$) as well as local convex hull estimator (LoCoH). Number of locations (*n*), number of intensive telemetry days (ITD; where locations were taken at hourly intervals), and number of days (D) the transmitter was on the air are also presented for each individual, and mean size of home range (± SE) are presented for each isopleth.

	n	ITD	D	KDE_{href}	$KDE_{ad hoc}$	$KDE_{plug-in}$	LoCoH
95% isopleth							
Adult							
m5	162	23	237	1.284	0.603	0.239	0.147
m7	115	17	104	1.532	0.744	0.355	0.233
m12	110	17	123	2.800	1.095	0.176	0.046
m16	83	13	144	13.790	4.298	0.665	0.285
m18	74	9	139	5.144	2.194	0.726	0.818
Mean				4.91 (2.32)	1.79 (0.69)	0.43 (0.11)	0.31 (0.13)
Juvenile							
m4	155	22	237	1.510	0.753	0.438	0.472
m6	143	21	195	3.091	1.405	0.363	0.133
m8	145	23	158	2.437	1.162	0.398	0.218
m9	149	23	206	0.708	0.382	0.170	0.070
m13	113	19	108	0.447	0.186	0.075	0.024
m17	57	11	83	3.335	1.349	0.321	0.214
Mean				1.92 (0.50)	0.87 (0.21)	0.29 (0.06)	0.19 (0.06)
Overall mean				3.28 (1.13)	1.29 (0.34)	0.36 (0.06)	0.24 (0.07)
50% isopleth							
Adult							
m5	162	23	237	0.253	0.077	0.020	<0.001
m7	115	17	104	0.348	0.112	0.051	<0.001
m12	110	17	123	0.620	0.195	0.013	0.006
m16	83	13	144	0.603	0.088	0.074	<0.001
m18	74	9	139	0.837	0.110	0.101	0.022
Mean				0.53 (0.10)	0.12 (0.02)	0.05 (0.02)	0.006 (0.004)
Juvenile							
m4	155	22	237	0.240	0.116	0.075	0.003
m6	143	21	195	0.600	0.134	0.043	<0.001
m8	145	23	158	0.346	0.117	0.049	0.001
m9	149	23	206	0.177	0.056	0.018	<0.001
m13	113	19	108	0.074	0.023	0.007	<0.001
m17	57	11	83	0.523	0.142	0.032	<0.001
Mean				0.33 (0.08)	0.10 (0.02)	0.04 (0.01)	0.001 (<0.001)
Overall mean				0.42 (0.07)	0.11 (0.47)	0.04 (0.01)	0.003 (0.002)

underestimated the use of space by constraining the estimate to within the boundaries of the points while excluding several locations from the 95% isopleth that were not excluded from other estimators' 95% isopleth (Table 1, Fig. 2). The average 95% isopleth home-range sizes in decreasing order were KDE_{href} (mean = 3.28 ha, SE = 1.13), $KDE_{ad\ hoc}$ (mean = 1.29 ha, SE = 0.34), $KDE_{plug-in}$ (mean = 0.36 ha, SE = 0.06), and LoCoH (mean = 0.24 ha, SE = 0.07) (Table 1). Using $KDE_{plug-in}$,
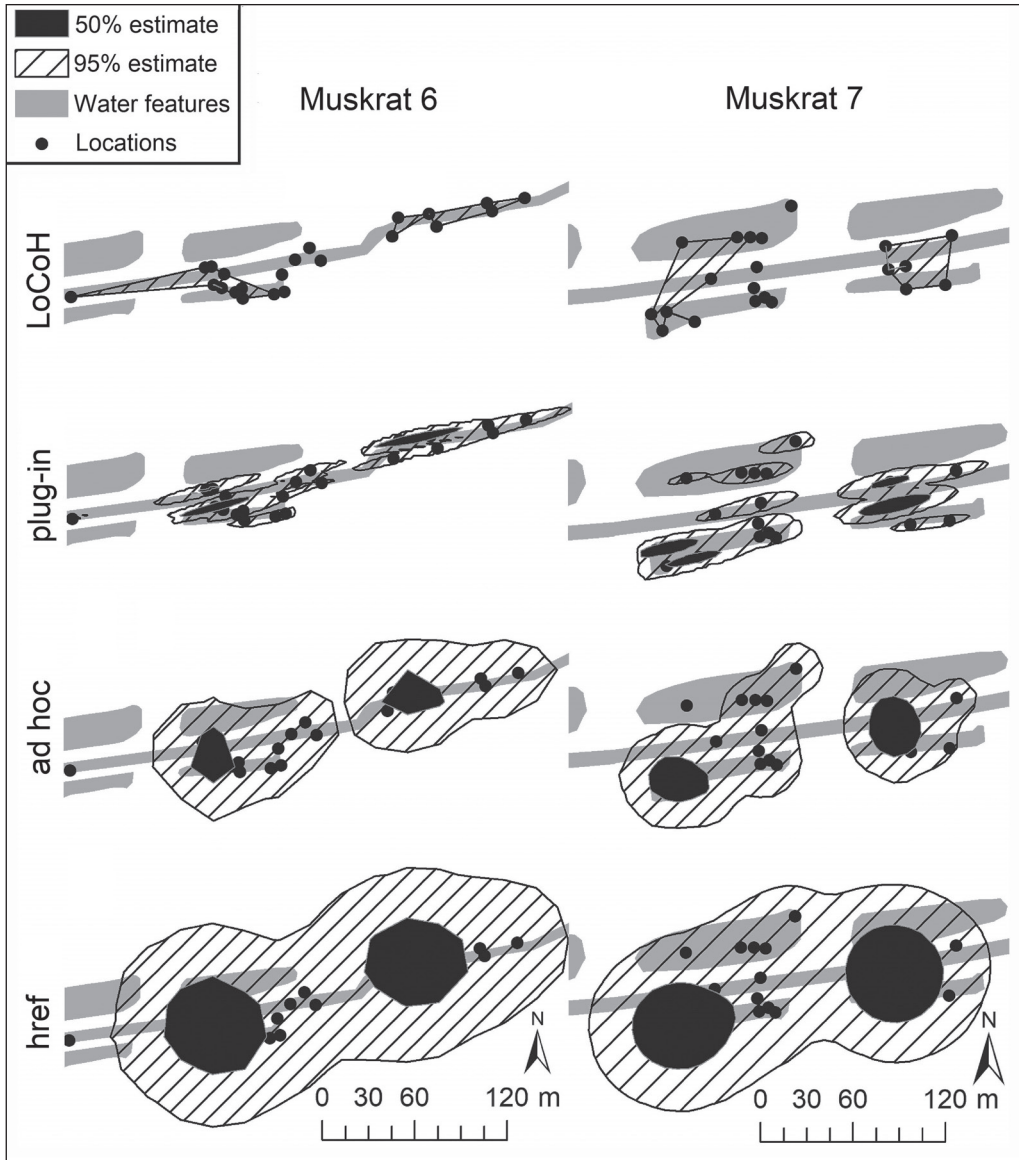

Figure 2. Comparison of all 4 (kernel density estimator [KDE]$_{href}$, KDE$_{ad\ hoc}$, KDE$_{plug-in}$, and local convex hull [LoCoH]) estimators of home range for the 95% and 50% isopleths for 2 individual *Ondatra zibethicus* (Muskrat) from August 2018 to February 2019. The pond–stream matrix in Lewisburg, PA, is depicted by the gray-shaded areas and labeled as water features.

an average of 68.57% (SE = 11.64, min–max = 0–98%) of an individual Muskrat home range overlapped other Muskrat home ranges. The average percent area of home-range overlap per age class was 56.84% (mean = 0.56, SE = 0.28) and 78.33% (mean = 0.78, SE = 0.27) for adults and juveniles, respectively.

Survival estimates

We calculated survival estimates based on encounter histories of 14 Muskrats. We were able to confirm predation as the cause of death for 6 individuals: 3 adults and 3 juveniles. We had 5 competing models with ΔAIC_c less than 2.0, with survival estimates varying from 0.58 to 0.67 (Table 2). To obtain relative variable importance, we calculated the sum of the weights of models containing each covariate. AVP had the highest total model weight ($\sum \omega_{AVP}$ = 0.60) and greatest support for influencing survival estimates, followed by age class ($\sum \omega_{age}$ = 0.41) then TDD ($\sum \omega_{TDD}$ = 0.28). The beta estimates for AVP indicated that survival was positively influenced by the average weekly precipitation (Table 3).

Table 2. Overwinter (8 November 2018–27 March 2019) survival estimates of Ondatra zibethicus (Muskrat) population (n = 14) in Pennsylvania for 8 known-fate models using an information-theoretic approach and ranked by ascending differences in Akaike's information criteria adjusted for sample size (ΔAIC_c). Models were calculated in the program MARK® and summary statistics reported are number of parameters (K), survival estimate with standard error in parentheses (S), model weight (ω_i), and the deviance of each model (D). Explanatory values are average total weekly precipitation (AVP), age class of Muskrat (age), and total degree days per week indexed around 0 ºC and standardized (TDD).

Model	K	S	ΔAIC_c	ω_i	D
S(AVP)	2	0.59 (0.16)	0.00	0.25	34.60
S(AVP + age)	3	0.66 (0.17)	0.65	0.18	33.17
S(.)	1	0.60 (0.15)	0.71	0.17	37.36
S(age)	2	0.67 (0.17)	1.38	0.12	35.98
S(AVP + TDD)	3	0.58 (0.16)	1.69	0.11	34.21
S(AVP + TDD + age)	4	0.65 (0.18)	2.52	0.07	32.94
S(TDD)	2	0.60 (0.15)	2.76	0.06	37.36
S(age + TDD)	3	0.67 (0.17)	3.45	0.04	35.97

Table 3. Intercept and beta estimates (SE) for 8 known-fate models of overwinter (8 November 2018–27 March 2019) survival of a *Ondatra zibethicus* (Muskrat) population (*n* = 14) in Pennsylvania calculated in the program MARK®. Models are ranked by ascending differences in Akaike's information criteria adjusted for sample size (ΔAIC_c). All covariates are standardized with mean of zero. AVP = average weekly precipitation; TDD = total degree days.

Model	Intercept	AVP	Age	TDD
S(AVP)	4.64 (1.28)	2.54 (2.25)		
S(AVP + age)	4.87 (1.34)	2.54 (2.27)	-0.67 (0.60)	
S(.)	1.25 (0.08)			
S(age)	3.89 (0.63)		-0.65 (0.60)	
S(AVP + TDD)	5.11 (1.73)	3.54 (3.17)		0.36 (0.58)
S(AVP + age + TDD)	5.16 (1.64)	3.20 (2.95)	-0.64 (0.61)	0.27 (0.58)
S(TDD)	3.66 (0.51)			-0.02 (0.49)
S(age + TDD)	3.89 (0.63)		-0.66 (0.60)	-0.06 (0.51)

Discussion

This is the first study in the eastern United States to successfully monitor Muskrat use of dwelling structures, movement, home-range size, and survival via implanted VHF radio-transmitters. Our observation of individual Muskrats using a large number of dwelling structures (mean = 9.17) is similar to other studies, particularly in the fall as Muskrats prepare for winter. Muskrats have been documented to exhibit more colonial behaviors in the fall than in the spring (Marinelli and Messier 1993), so it is not surprising that both juvenile and adult Muskrats cohabited dwelling structures in our study. For instance, we recorded up to 8 individuals using the same burrow simultaneously. Although we were unable to determine genetic relationships between individuals, it is likely many of them were related. In a marsh in Ontario, researchers observed the use of 1 to 6 active huts per Muskrat family group using mark–recapture data (Proulx and Gilbert 1984). In contrast, Schooley and Branch (2006), using radio telemetry, observed *Neofiber alleni* True (Round-tailed Muskrat) using 10–15 dwelling structures in freshwater marshes of Florida. Most of the previous studies conducted on Muskrat use of dwelling structures and movements used mark–recapture techniques or visual observations. We documented use of dwelling structures by employing radio-telemetry equipment, a feasible technique that allowed us to track animals both swimming and burrowing that would once have been extremely difficult using visual observation alone. Our data supports previous research that Muskrats share a large amount of space, especially dwelling structures, with other Muskrats (Ching and Chih-tanc 1962, Marinelli and Messier 1993).

We also observed Muskrats moving relatively short distances (28 m/hr) in the fall, remaining at or near lodges much of the time (i.e., 79% of all telemetry locations were at dwelling structures). Muskrats spent a short amount of time moving across the landscape and only moved a mean distance of 28 m when moving to a new location. Due to the limitations of VHF telemetry, we were only able to determine rough estimates of distance moved between 2 points. While our estimates do not accurately reflect the total distance moved in 1 hour, they do imply that the relocation of an individual after 1 hour will likely occur nearby the previously collected location. Muskrats in this isolated population appeared to spend the majority of their time in close proximity to one another. Although the movement data we collected only encompasses fall and winter, this is also the period when movement is likely reduced as Muskrats prepare for winter and their movement is limited by ice cover. Understanding how landscape-scale habitat configuration influences localized hourly movements needs to be further explored, as does movement patterns in other seasons, because all have implications towards potential for disease spread and transmission with a communal denning species such as Muskrat.

Our assessment of 4 estimators identified considerable differences in each estimator's ability to capture size and shape of Muskrat home range. Because Muskrats burrow along banks of waterways, they often "outline" habitat boundaries, making LoCoH a viable option for calculating size of Muskrat home ranges in linear habitats. In open marshes or ponds, or combinations of linear habitats and circular

habitat (e.g., lakes, marshes); however, LoCoH underestimates the space use within non-linear habitats. Furthermore, the 95% isopleth for LoCoH did not include 37% of locations for 1 Muskrat (Fig. 2). Conversely, KDE_{href} overestimates space use of Muskrats in linear habitats. We calculated distance from non-dwelling locations to water bodies, and none of the locations were farther than 10 m from the edge of a water body. The shape of the 95% isopleth using KDE_{href} expanded beyond the non-dwelling distance we observed for locations collected. The $KDE_{ad\ hoc}$ estimator appeared to be a more appropriate representation of Muskrat home ranges than KDE_{href}, although it still appeared to overestimate the area used. To adequately accommodate use of water sources of various shapes and configurations by Muskrat, we utilized $KDE_{plug-in}$ to constrain the estimate to the boundaries of the habitat. The $KDE_{plug-in}$ performed well when estimating size of home range within a combined linear and non-linear matrix characteristic of the pond–stream complex at our site. For example, 1 individual (m16) dispersed ~750 m upstream from the pond where all of its locations were taken during the fall months. The estimates for that same individual using KDE_{href} and $KDE_{ad\ hoc}$ were 6–19 times larger than those of the $KDE_{plug-in}$ (13.79 ha, 4.30 ha, and 0.66 ha, respectively) and extended upwards of 130 m into uninhabitable land (i.e., parking lots and shopping centers). Thus, it is important, especially for semi-aquatic and aquatic organisms, to take habitat availability into consideration when selecting an estimator of home range to adequately determine size and shape. Using $KDE_{plug-in}$ over the other 3 estimators would appear more reliable in order to appropriately estimate the size and shape of a Muskrat home range, as well as for use in analyses of space use such as percent area overlap.

Our estimate of 69% home range overlap using home ranges from the $KDE_{plug-in}$ is a conservative estimate of percent area overlap because we did not capture all individuals within the population. For instance, 1 Muskrat was seen foraging in tandem with 3 other Muskrats on multiple occasions, and none of the other Muskrats were radio-tagged. Our findings of 69% overlap is comparable to the 75% overlap finding in the study conducted by Ching and Chih-tanc (1962). A greater percentage of home-range overlap is expected in areas with high population density, especially in a constrained habitat and for semi-colonial species such as Muskrat. In conjunction with our finding that Muskrats spend the majority of their time in dwelling structures with other Muskrats, our observation that over half of an individual home range overlaps that of several other Muskrats further supports concerns about the potential for disease transmission within local populations.

Along with this increased potential for disease transmission, areas of high density may also facilitate predation events (Niemuth and Boyce 1995). The only source of mortality we observed in radio-tagged Muskrats was predation by Mink (n = 6). We did not observe any disease-related mortality in the radiomarked Muskrats; however, all carcasses were scavenged prior to recovery, and we were unable to ascertain the condition of the Muskrat prior to the predation event. High predation by American Mink in our study may suggest an anecdotal increase in Mink populations in Pennsylvania suggesting that larger populations of Mink leading to increased predation pressure might be affecting Muskrat populations.

However, estimated Mink and Muskrat harvests have been following a parallel decline from 1985 to 2018 (see Supplemental File 1; AFWA 2017). Viljugrein et al. (2001) also observed similar trends with no lag time between Mink and Muskrat harvest rates in eastern Canada, suggesting weak predator–prey interactions. Since most Muskrat trapping sets also capture Mink, we would have expected to see an increase in Mink harvest if Mink populations were indeed on the rise. Muskrats are an r-selected species that can produce multiple, moderate-sized litters in 1 year. In turn, the number of offspring produced should counter the number of predation events observed. There are numerous predators of the Muskrat, however, so we cannot directly dismiss the impact of predation on Muskrat populations. Our observation of frequent predation by Mink at our site merely suggests that further research is needed to determine if such predation represents additive mortality on Muskrats in Pennsylvania.

Ahlers et al. (2010b) documented that flooding events during heavy precipitation from July to November did not affect survival; however, they did not monitor effects of precipitation during the winter months. Our findings imply that there are seasonal differences in the effect of precipitation on survival. However, we were unable to follow Muskrats through ice melt in spring when survival is likely impacted by additional predation events, and the standard errors of our model coefficients were large, resulting in poor prediction of Muskrat survival, most likely due to small sample size. Most of the precipitation occurring during our study was snowfall and may correlate to low Muskrat activity outside of their dwelling structures. Unlike rain, snowfall on frozen water bodies would not cause a drastic increase in water levels that would typically result in Muskrats being flushed out of their burrows. Trends in winter precipitation and season length have changed in the past half-century. For example, the time between the first and last days in a snow year shortened from 1950 to 2010 in most of the United States except for several midwestern states (Knowles 2015). Coincidentally, observations of higher rates of Muskrat harvest declines are located in states where Knowles (2015) reported snow-year lengths shortening (Ahlers and Heske 2017). To receive and accumulate snowfall, air temperatures need to be low, and therefore might be correlated with ice formation on water bodies. Ice may create a safety barrier for Muskrats during the winter months and may be positively correlated with survival provided ice thickness does not result in "freeze out", where Muskrat movements are restricted and their food supply becomes encased in ice.

We acknowledge that our small sample size and limited sampling area impacts our ability to make inferences about our results as they relate to overall Muskrat populations. With limited transmission range (<100 m) requiring observers to track individuals in close proximity, we also acknowledge that homing in on foraging Muskrats may have potential observer influences on Muskrat behavior and movements. However, we present a preliminary assessment of the ecology of a small urban Muskrat population and provide inferences on dynamics that may be observed in similar areas. Furthermore, the presence of novel or introduced pathogens and parasites into a system would require a basic understanding of Muskrat denning characteristics, space use, and survival in the way that we present here.

Acknowledgments

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