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Using Harvest Data to Assess Factors Influencing Regional Population Declines of Muskrats (*Ondatra zibethicus*)

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ABSTRACT

Although muskrats (*Ondatra zibethicus*) provide ecological, economic, and cultural values to wetlands, populations have experienced declines throughout North America. The cause(s) of declines remain unclear but may be linked to wetland loss, fragmentation, or degradation; weather; or diseases. We used harvest data from the Midwest, USA, as an index of abundance to investigate factors influencing population declines. Using linear mixed-effects models, county-level harvest of muskrats was positively associated with wetland connectivity and size, suggesting that population declines may be related to wetland loss. Site-level harvest was positively influenced by wetland habitat conditions, though additional studies may be necessary to corroborate this pattern. Wetland-restoration efforts directly benefiting muskrat habitat may also benefit other wetland-obligate wildlife communities. Strategies for managers include increasing the value of data collected during annual fur-harvester surveys (e.g., standardization) to more effectively monitor muskrat demographics and help reveal specific factors affecting population trends.

1 | Introduction

Despite providing ecosystem services and habitat for numerous wildlife species (Costanza et al. 1997; Zedler and Kercher 2005), wetlands across the United States have experienced a loss of > 53% since the late 18th Century (Dahl and Allord 1996; Mitch and Gosselink 2007). Muskrats (*Ondatra zibethicus*) are important ecosystem engineers and indicators of ecosystem health in wetland communities (Higgins and Mitsch 2001; Ahlers et al. 2020; Aarrestad et al. 2021; Bomske and Ahlers 2021). Muskrats can retard growth of wetland vegetation, including cattails (*Typha* spp.), through intense herbivory (Smirnov and Tretyakov 1998; Clark 2000; Erb and Perry 2003; Nummi et al. 2006; Kua et al. 2020), improving conditions for other wetland wildlife, including amphibians, fish, invertebrates, marsh birds, and waterfowl (Kaminski and Prince 1981; Nelson and Kadlec 1984; de Szalay and Cassidy 2001; Nummi et al. 2006). For example, hemi-marsh conditions created and maintained by muskrats result in a mix of open water and vegetative structure that provides nesting and loafing areas for migrating waterfowl and waterbirds.

Recent empirical evidence suggests declines in muskrat populations are widespread and long-term, including within the Midwest United States (Toner 2006; Ahlers and Heske 2017; Ward and Gorelick 2018; Sadowski and Bowman 2021). These population declines could reflect issues in wetland systems that also negatively impact other wetland fauna, including those that benefit directly or

Summary

Practitioner Points

- Regional population declines of muskrats have been occurring across North America for several decades.
- Using harvest data as an index of population abundance, populations may be declining due to loss of wetland connectivity and decreasing wetland size.
- Standardized surveys of muskrat harvest would yield more effective monitoring of muskrat populations.

indirectly from muskrat activities (Erb and Perry 2003; Wilcox and Xie 2008). Lastly, muskrats are an important contributor to both the economic and cultural components of the international fur trade (Novak et al. 1987; Association of Fish and Wildlife Agencies 2022).

Although mechanistic explanations are currently unknown for the long-term decline in muskrat populations, some plausible hypotheses exist (Ahlers and Heske 2017). Wetland loss and degradation have likely negatively affected muskrats and other species by altering vegetation dynamics in wetlands, reducing population connectivity, and limiting the availability and amount of high-quality habitat (Clark 2000; Erb and Perry 2003; Ervin 2011; Ward and Gorelick 2018; Sadowski and Bowman 2021). Similarly, apparent declines in muskrat populations since the mid-1980s (Roberts and Crimmins 2010; Ahlers and Heske 2017) have occurred simultaneously with increasing variability and extremity in precipitation events (Melillo et al. 2014). Muskrats are sensitive to increasing frequency, intensity, and duration of drought and flooding events (Bellrose and Low 1943; Piha et al. 2007; Ahlers et al. 2015), which can affect food availability (Clark and Kroeker 1993), recruitment (Kinler et al. 1990), displacement (Ahlers et al. 2015), and metapopulation dynamics (Straka et al. 2018; Ward et al. 2021). Finally, increased exposure to contaminants in degraded wetlands may also reduce survival and reproduction of muskrats (Ohio Department of Natural Resources 2016).

No single factor has been identified as the driver of declining populations, and little information exists as to how these factors may work synergistically or vary spatially across the geographic distribution of muskrats. Therefore, we conducted a regional evaluation of relationships between muskrat abundance, as indexed by harvest data, and a set of factors through analysis of multi-year, multi-spatial-scale data sets collected throughout the Midwest, USA. Our objectives were to: (1) evaluate if harvest data relate to wetland condition, quality, and spatial attributes, along with weather, land-cover type, and other factors; and (2) investigate factors associated with apparent population declines in the Midwest. We hypothesized that factors associated with wetland condition, size, and connectivity (i.e., distance between wetlands) would be important contributors to annual population abundance (as indexed by annual harvest).

1.1 | Study Area

Our study area included Michigan (MI; 250,487 km^2), Minnesota (MN; 225,163 km^2), Ohio (OH; 116,098 km^2), and Wisconsin (WI; 169,635 km^2), USA (Figure 1). This area is characterized primarily by two ecoregions: Eastern Temperate Forest and Northern Forest (Omernik and Griffith 2014). The Northern Forest ecoregion has relatively dense forested areas and low population densities of humans, whereas the Eastern Temperate Forest has relatively greater agricultural land cover and greater population densities of humans (Danz et al. 2007). The Great Plains ecoregion occurs adjacent to the Great Lakes Basin restricted primarily to western and southern Minnesota, and is characterized by agricultural land use, relatively flat, dry terrain, and grasslands (Omernik and Griffith 2014). Elevation ranges from 138.7 m in southwestern Ohio to 701.3 m in northeastern Minnesota (US Geological Survey 2026). Mean annual precipitation generally increases west to east, and ranged from 53.9 cm (MN) to 80.1 cm (OH); mean daily temperature generally increases from south to north, and ranged from 5.6°C (MN) to 11.0°C (OH) during 2000–2018 (Midwest Regional Climate Center 2026).

2 | Methods

2.1 | Harvest Data

Harvest data represent a valuable tool to assess muskrat population trends, and often represent the only long-term and geographically widespread data sets for many furbearing species (White et al. 2015; Ahlers and Heske 2017; Hiller et al. 2018, 2021; Ahlers et al. 2021). Inherently, harvest is linked to local or regional abundances of species (McKelvey et al. 2011; Ahlers et al. 2016). When assessing harvest data, the potential influence of trapper effort must be addressed to ensure biological factors influencing species abundance are disentangled from trapper effort (Landholt and Genoways 2000; DeVink et al. 2011; McKelvey et al. 2011; Ahlers et al. 2016). If trapper effort is not quantified directly, then factors influencing trapper effort must be identified and controlled for during analysis (DeVink et al. 2011; McKelvey et al. 2011; Ahlers et al. 2016).

We used harvest information from state and federal biologists responsible for managing furbearer populations within our study area. We used two spatial scales for our analyses: (1) county-level harvest obtained from statewide fur-harvester surveys in Michigan, Minnesota, and Ohio, and (2) site-level harvest data obtained from sites within state-managed areas and the US Fish and Wildlife Service (USFWS) National Wildlife Refuge System. For each spatial scale, we evaluated two separate model sets, one set using all available years of data, but excluding variables associated with wetland-vegetation characteristics, and one set using data collected during 2011–2018, which was of shorter duration but provided available wetland-vegetation data. For county-level analyses, we obtained data collected by Michigan Department of Natural Resources (2025), Minnesota Department of Natural Resources (2025), and ODNR (2025) via voluntary surveys mailed to a subset of licensed trappers to assess muskrat harvest. Specific questions related to trapper effort varied by state (Supporting Information S1: Table S1).

For our site-level analyses, we compiled a series of data sets detailing annual muskrat harvest from 18 state-managed areas and 8 national wildlife refuges in Michigan, Minnesota, Ohio, and Wisconsin (Supporting Information S1: Tables S2 and S3). Methods for collecting data varied by site and agency, but generally followed site-specific protocols that consisted of post-season surveys of trappers. Reporting requirements (i.e., mandatory or voluntary) varied by site. For each site, we consulted site managers about collection methods, data quality, and limitations. Based on these discussions, we included data sets only from sites: (1) where number of trappers/year could be quantified and assigned to corresponding annual harvest data, (2) with > 5 seasons of muskrat-harvest data, and (3) where date range of harvest data was 2000–2018 (Supporting Information S1: Tables S1–S3). We summarized all site-level data sets excluded from analyses and described our rationale (Supporting Information S1: Table S3). Within our data sets, no regulations for any site or state included a harvest limit for muskrats.

2.2 | County-Level Harvest

Our ability to directly quantify trapper effort differed based on specific questions asked within fur-harvester surveys (Supporting Information S1: Table S1). For example, although information on number of traps set specifically for muskrats was available for Minnesota and Ohio, these data were not included within surveys of trappers in Michigan. Therefore, we developed a common index for harvest (i.e., per-capita harvest of muskrats). In our analysis of county-level per-capita harvest of muskrats, we combined data from each of the three states into a single data set. We defined our dependent variable of per-capita harvest of muskrats (PCHM) for each county and harvest season as:

$$\mathrm{PCHM} = \frac{\sum \mathrm{Harvest}_i}{\sum \mathrm{Trappers}},$$

where $\mathrm{Harvest}_i$ = number of muskrats reported as harvested by an individual trapper (i), and Trappers = number of trappers reporting muskrat harvest.

When calculating PCHM from surveys, we excluded any data that contained errors, such as an individual trapper that reported number of days greater than available in a given harvest season, grammatical errors affecting interpretation of data, or otherwise incomplete data. For survey responses in which multiple counties were listed for muskrat harvest, we equally proportioned values among relevant counties. To test our hypotheses related to factors influencing the population dynamics of muskrats, we included existing data collected within our study area by several sources. We used only data considered biologically meaningful to county-level scale of harvest data and of sufficient temporal and spatial completeness (Supporting Information S1: Tables S4 and S5).

We developed a set of county-level variables associated with annual weather patterns to evaluate influences of temperature, precipitation, and drought on muskrat harvest and population dynamics (Supporting Information S1: Table S4). We calculated annual deviation from the previous 10-year averages in monthly temperature (°C) and precipitation (cm) during summer months (Jun–Aug) immediately preceding a given harvest season and during winter months (Dec, and Jan, Feb of following year) during a given harvest season. We obtained temperature and precipitation data from a 4-km grid cell located near the centroid of each county (PRISM Climate Group 2021). We also calculated the annual Palmer Drought Severity Index and Standardized Precipitation Index averaged across the spatial extent of each county for the year (t) of initiation of each harvest season ($\mathrm{Drought}_t$ and Precip_t, respectively), and for the preceding year ($\mathrm{Drought}_{t-1}$, Precip_{t-1}). Data for Drought and Precip were obtained from gridded data sets of surface meteorological variables (gridMET data set; Abatzoglou 2013) and were extracted for each county using Climate Engine (Huntington et al. 2017).

We defined a set of variables to quantify landscape-scale land-cover and spatial attributes of wetlands associated with each county (Supporting Information S1: Table S4). Using the land-cover types within National Land Cover Database (NLCD; Multi-Resolution Land Characteristics Consortium 2021), we estimated the total area (%) of each of the three land-cover types (open water, woody wetland, and emergent herbaceous wetland) associated with wetlands within each county for each of the 7 years (2001, 2003, 2006, 2008, 2011, 2013, and 2016) in which these data were consistent with our study period. We also combined a subset of existing land-cover types to create three additional categories to define broader-scale land-cover types including: (1) wetlands (open water, woody wetlands, and emergent herbaceous wetlands); (2) agricultural (pasture-hay and cultivated crops); and (3) developed (developed open space, developed low intensity, developed medium intensity, and developed high intensity). We then calculated the total area (%) within each county for each category.

We used the wetlands category to estimate variables for mean area of all wetland patches (Patch Area), largest area of a wetland patch (Largest Patch), mean Euclidean nearest-neighbor distance (m) between wetland patches (Connectivity), and number of wetland patches (Number of Patches) within each county using the landscapemetrics package (Hesselbarth et al. 2019) in Program R v. 4.5.0 (R Core Team 2025). We defined size of individual patch as a single raster cell based on the spatial resolution (30 m) of NLCD. For all land-cover variables derived from NLCD, we used linear interpolation to estimate values during years when NLCD data were not available. We used the National Wetland Inventory (NWI) database to estimate total area (%) of different wetland types within each county (USFWS 2021). Data from the NWI are continuously updated, resulting in values for these variables being fixed in time (i.e., no variation on an annual basis) within our data set. Finally, we assigned each county to one of three ecoregions (Eastern Temperate Forest, Great Plains, Northern Forest; Omernik and Griffith 2014). For any counties that included > 1 ecoregion, we assigned the ecoregion with the greatest area (%) within that county.

To evaluate effects of wetland vegetation on muskrat harvest, we interpolated variables for floristic quality index (Floristic; calculated by summing coefficients of conservatism of each species presence and dividing that value by the square root of species richness) and vegetative multimetric index (VegI; an index of 0–100 calculated using Floristic, relative importance of native plants, tolerance to disturbance, and relative cover of

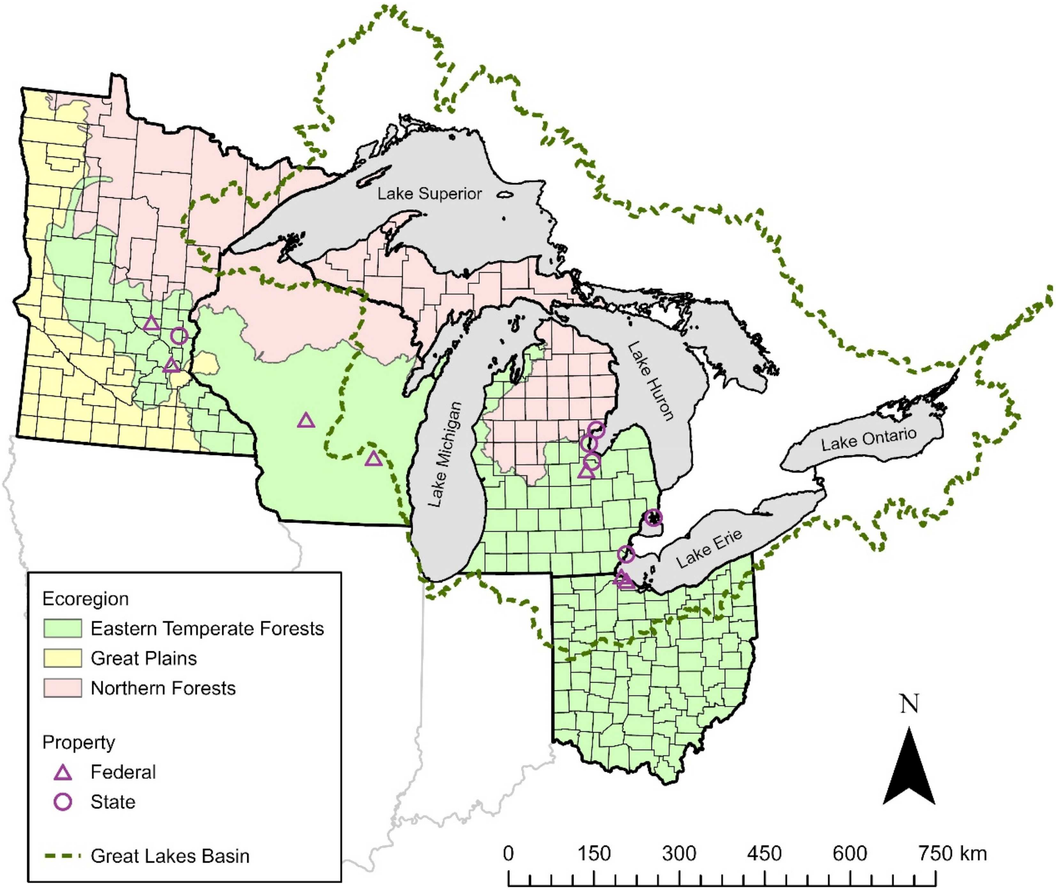

FIGURE 1 | Study area for analysis of site- (state-managed areas [$n = 6$], national wildlife refuges [$n = 7$]) and county- ($n = 258$) level harvest data for muskrats (*Ondatra zibethicus*) in Michigan (2007–2018), Minnesota (2000–2018), Ohio (2008–2018), and Wisconsin (2001–2018), USA, including boundary for the Great Lakes Basin, and the distribution of Ecoregions (level I; Omernik and Griffith 2014).

native monocot species; Magee et al. 2019, U.S. EPA 2024a:114, 145) based on data derived from three programs associated with wetland assessment and monitoring within our study area. These programs included the National Wetland Condition Assessment (NWCA) conducted by the US Environmental Protection Agency (2024a, 2024b), the Wetlands Rapid Assessment Monitoring program (ORAM) conducted by Ohio Environmental Protection Agency (OH EPA; Gara and Schumacher 2015), and the Minnesota Wetland Condition Assessment (MWCA) conducted by the Minnesota Pollution Control Agency (MPCA; Bourdaghs et al. 2019) during either 2011 or 2012 and 2016, depending on location and data source. We used kriging interpolation to create predictive contours for both Floristic and VegI for our study area using the gstat package (Pebesma 2004; Gräler et al. 2016) in Program R. We then assigned Floristic and VegI values to each county based on the mean value of the predicted contours within each county. For data collected by NWCA and ORAM, Floristic and VegI were available only for 2 years (either 2011 or 2012 and 2016) during our study period. Therefore, we ran a subset of models using data during 2011–2018. VegI and Floristic were excluded from the full data set because no data were available prior to 2011. For both Floristic and VegI, vegetation condition of wetlands was considered to be more representative of native, undisturbed plant communities at higher values compared to non-native, disturbed communities at lower values (Magee et al. 2019; U.S. EPA 2024a, 2024b).

Because effort was not directly quantified in our dependent variable (i.e., PCHM), we calculated independent variables annually for gasoline price, pelt price, and unemployment rate, each of which may influence trapper effort (Ahlers et al. 2016). We obtained data from annual fur-buyer surveys conducted in Minnesota (MNDNR, unpubl. data), Michigan (C. Kettler, Michigan Trappers and Predator Callers Association, unpubl. data), and Ohio (ODNR, unpubl. data) to calculate mean pelt prices (US$) for muskrats in each state. We also obtained mean statewide annual retail price (US$) for all gasoline formulations (gasoline price) for each state (U.S. Energy Information Administration 2021). We adjusted both pelt price and gas price for inflation each year based on the Consumer Price Index for 2018 (U.S. Bureau of Labor Statistics 2021). Finally, we calculated mean annual statewide unemployment rate for each state (U.S. Bureau of Labor Statistics 2021).

We used linear mixed-effects modeling (LMM) to evaluate relationships between PCHM and our set of independent variables associated with each analysis. To avoid multicollinearity, we used the Pearson product-moment correlation coefficient (r) and did not include variables in the same model that were highly correlated ($|r| > 0.7$; Sheskin 2007). We used natural-log transformations for our dependent variables because residual diagnostics indicated misspecification in Poisson and negative-binomial count models with offsets. We rescaled all of our continuous independent variables by centering and dividing by

TABLE 1 | Model-selection results of the 10 highest-ranked models within a set of 52 models for analysis of muskrat (*Ondatra zibethicus*) harvest using annual county-level data collected for all counties ($n = 258$) in Michigan (2000–2018), Minnesota (2002–2018), and Ohio (2008–2018), USA. Dependent variable was per-capita harvest of muskrats. Models are ranked based on Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002), where K = number of model parameters, LL = log-likelihood value of model, ΔAIC_c = difference in AIC_c relative to highest-ranked model within the model set, and $w = AIC_c$ weight. Random effects included County and Harvest Season, and extrinsic fixed-effect variables included Pelt Price, Gasoline Price, and Unemployment Rate included for all models. * = pairwise interaction terms.

Model	K	LL	ΔAIC_c	w
Connectivity * Ecoregion + $Precip_t$ * Ecoregion + $Precip_{t-1}$ * Ecoregion	18	−4324.71	0.00	0.76
Area Wetland * Ecoregion + $Precip_t$ * Ecoregion + $Precip_{t-1}$ * Ecoregion	18	−4326.26	3.11	0.16
Area Woody Wetlands * Ecoregion + $Precip_t$ * Ecoregion + $Precip_{t-1}$ * Ecoregion	18	−4327.41	5.40	0.05
Winter Temp * Ecoregion + $Precip_t$ * Ecoregion + $Precip_{t-1}$ * Ecoregion	18	−4327.98	6.55	0.03
$Precip_t$ * Ecoregion + $Precip_{t-1}$ * Ecoregion	15	−4336.81	18.15	< 0.01
Summer Temp * Ecoregion + $Precip_t$ * Ecoregion	15	−4350.18	44.89	< 0.01
Winter Temp * Ecoregion + $Precip_t$ * Ecoregion	15	−4350.74	46.00	< 0.01
Connectivity + $Precip_t$ + $Precip_{t-1}$ + Ecoregion	12	−4364.23	66.94	< 0.01
$Precip_t$ + $Precip_{t-1}$ + Ecoregion	11	−4366.03	68.53	< 0.01
Summer Temp * Ecoregion + Winter Temp * Ecoregion	15	−4369.54	83.60	< 0.01

1 standard deviation to aid model convergence and interpretation (Schielzeth 2010). In all models in each model set, we included categorical variables county and harvest season as random effects.

We constructed a set of *a priori* models by logically grouping variables, including interaction terms when appropriate. Each of our model sets additionally included a null model. We included extrinsic variables related specifically to trapper effort (i.e., gasoline price, pelt price, unemployment rate) in all models within this set. Because effort directly affects observed counts, they were included in every model as a control variable. This means our baseline model was not a true intercept-only null, but a minimum model that accounts for effort.

We assessed the fit of our model sets through residual diagnostics on scaled residuals using a simulation approach with the DHARMa package (Hartig 2021) in Program R. We used Akaike Information Criterion adjusted for small sample size (AIC_c) to rank models based on model complexity and fit (Burnham and Anderson 2002), and considered variables in the highest-ranked models with 95% confidence limits that did not overlap zero to have strong support in describing our independent variable. We performed all statistical analyses using Program R.

2.3 | Site-Level Harvest

We expected many of the same variables described for assessing county-level muskrat harvest would potentially influence site-level harvest. Therefore, we used the same set of variables for all site-level analyses, but adjusted the spatial scale to more appropriately represent the scale of this analysis. For weather-related variables, we calculated annual values from the 4-km grid cell located at the center of each site (i.e., those associated with temperature and precipitation) or averaged within site boundaries (i.e., annual Drought and Precip). For those variables associated with land cover and wetland vegetation index, we calculated each variable across a spatial extent that included the area contained within 10 km of the boundaries of each site to account for attributes of the adjacent landscape. For gasoline price, pelt price, and unemployment rate, we used state-level values and included an effort-only model in all model sets to represent a minimum model.

Because only two of the site-level data sets for muskrat harvest directly quantified trapper effort, we used PCHM while controlling for extrinsic factors influencing trapper effort as our dependent variables to standardize comparisons across sites. We used generalized linear mixed models (GLMM) to evaluate the relationship between PCHM and the set of independent variables for each site. We transformed PCHM using a natural-log transformation and rescaled all of our continuous independent variables by centering and dividing by 1 standard deviation to aid model convergence and interpretation (Schielzeth 2010). For all models within both model sets, we included the categorical variables site and harvest season as random effects. We constructed a set of *a priori* models by logically grouping variables, including interaction terms when appropriate. Each of our model sets included an effort-only model. Similar to our regional analysis of PCHM, we included effects of gasoline price, pelt price, and unemployment rate in all models to account for trapper effort. We assessed model fit and performance using methods similar to those for county-level analysis.

3 | Results

3.1 | Harvest Data

Our regional analysis of county-level muskrat harvest included 258 counties within three states (MI, MN, OH), where a combined total of 1,849,528 harvested muskrats were reported by 43,512 trappers during 2000–2018. Reported number of muskrats harvested, number of trappers, and date ranges of available data varied by state (Supporting Information S1: Table S6). Using harvest data collected during only 2011–2018 resulted in 971,155 harvested muskrats reported by 21,421 trappers. After filtering data, our site-level analyses contained harvest data from six state-managed areas and seven national wildlife refuges (Figure 1, and Supporting Information S1: Table S2). Throughout these 13 sites, 324,245 harvested muskrats were reported by 1339 trappers in state-managed areas, and 138,668 harvested muskrats were reported by 595 trappers in national wildlife refuges during 2011–2018. The date ranges of site-level data on muskrat harvest included in our model set varied by site (Supporting Information S1: Table S2).

3.2 | County-Level Harvest

Several of our independent variables were correlated, including Drought_t and Precip_t ($r = 0.87$), Drought_{t-1} and Precip_{t-1} ($r = 0.87$), Floristic and VegI ($r = 0.76$), and many of our variables assessing wetland distribution based on NLCD with those based on NWI ($r > 0.70$). Because each pair of correlated variables represented variables quantifying a similar underlying attribute, we removed one variable in each pair from further analysis to reduce redundancy and to aid model interpretation. Specifically, we removed Drought_t, Drought_{t-1}, Floristic, and NWI variables from consideration, and retained Precip_t, Precip_{t-1}, VegI, and NLCD variables.

Our highest-ranked model from our county-level model set using all years of data contained pairwise interactions between Connectivity, Precip_t, and Precip_{t-1} with Ecoregion (Table 1 and Supporting Information S1: Table S7). PCHM was inversely associated with distance between wetland patches in the Eastern Temperate Forest ecoregion. Specifically, PCHM predictions ranged from 27.63 (95% CL = 23.81–32.07) at the shortest recorded distance (114.57 m) between wetland patches to 17.72 (95% CL = 13.16–23.85) at the greatest distance (644.51 m) between wetland patches while holding all other variables constant at their respective mean values. In the Northern Forest ecoregion, there was a decrease in PCHM, with predictions ranging from 22.24 (95% CL = 15.78–31.35) at the shortest distance (74.25 m) between wetland patches to 9.15 (95% CL = 6.35–13.18) at the greatest distance (154.89 m) between wetland patches. In the Great Plains ecoregion, PCHM increased from 15.90 (95% CL = 10.88–23.23) at 103.04 m between wetlands to 52.93 (95% CL = 34.61–80.96; Figure 2) at 344.98 m between wetlands. PCHM was positively related to Precip_t for all ecoregions, whereby the intercept and strength of each relationship varied by Ecoregion (Supporting Information S1: Figure S1). PCHM decreased in the Eastern Temperate Forest with increased Precip_{t-1} but increased in the Northern Temperate and Great Plains ecoregions with increased Precip_{t-1} (Supporting Information S1: Figure S2). All effort variables in the top-selected model were strongly associated with PCHM, where PCHM increased with increasing pelt price (0.12; 95% CL = 0.07–0.16) and increasing unemployment rate (0.07; 95% CL = 0.02–0.11), and declined with average gas price (−0.07; 95% CL −0.11– −0.02). The minimum model of effort only was not ranked in the top ten models (ΔAIC = 140.26, $w = 0.00$).

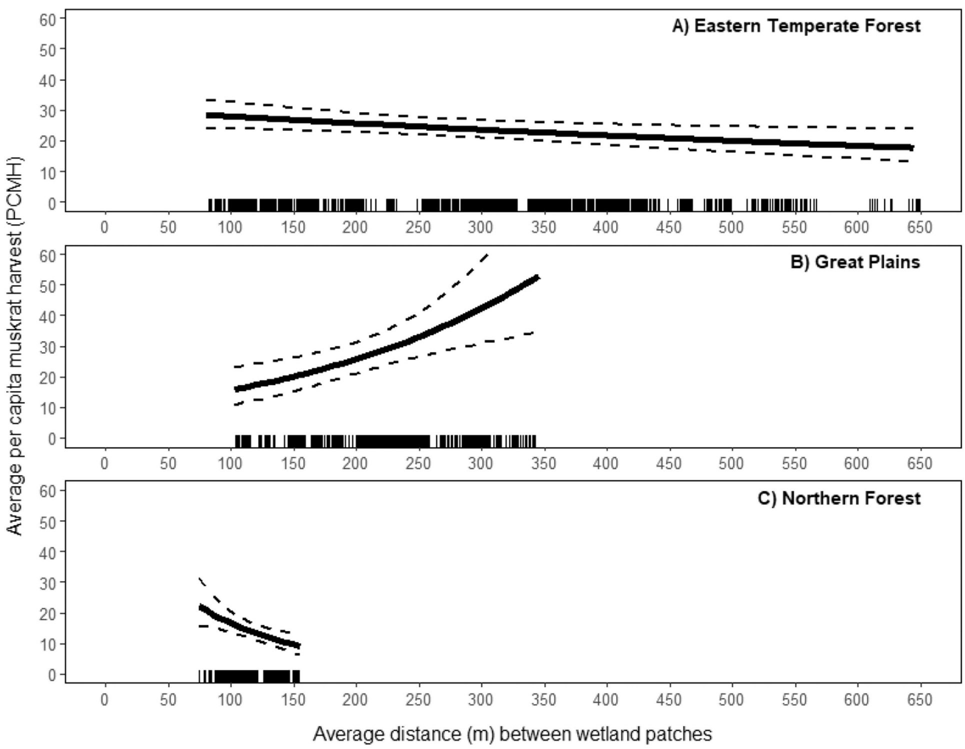

FIGURE 2 | Relationship between annual reported per-capita harvest of muskrats (*Ondatra zibethicus*; PCHM) by county and mean distance (m) between wetland patches (Connectivity)/county by ecoregion: (A) Eastern Temperate Forest, (B) Great Plains, and (C) Northern Forest. Annual county-level harvest data were based on fur-harvester survey data collected in Michigan (2007–2018), Minnesota (2000–2018), and Ohio (2008–2018), USA. Back-transformed relationship (solid lines) and 95% confidence limits (dashed lines) were predicted from the highest-ranking model based on Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) from a model set containing 52 models where all other model variables were held at their mean value. Data included 3682 county-harvest season combinations. Distribution of actual values for Connectivity are shown as a rug plot along the *x*-axis for each panel, respectively. Refer to text for parameters and model estimates (15 parameters).

The highest-ranked model for the county-level model set (2011–2018) included an additive effect of Winter Temp and pairwise interactions between $Precip_t$, and $Precip_{t-1}$ with Ecoregion (Supporting Information S1: Tables S8 and S9). PCHM increased by 21.5% (95% CL = 14.9–28.5) with each increase of 1 standard deviation (2.61) in the winter temperature deviation from the 10-year average (Supporting Information S1: Figure S3). PCHM was positively associated with $Precip_t$, particularly in the Eastern Temperate Forest and Great Plains, with smaller increases in the Northern Forest (Supporting Information S1: Figure S4). PCHM also increased with increased $Precip_{t-1}$ with varying strength across all ecoregions (Supporting Information S1: Figure S5). The only supported effort variable in the top selected model was gas price which was positively associated with PCHM (0.24 95% CL = 0.13–0.35). The minimum model of effort received no support (ΔAIC = 96.36, w = 0.00).

3.3 | Site-Level Harvest

At the site level, we included 13 sites (area = 18.9–481.2 km^2) within state- and federally (i.e., National Wildlife Refuge System) managed areas in four states (MI, MN, OH, WI; Figure 1). Twelve sites were located in the Eastern Temperate Forest, and one site in the Northern Forest. The same pairs of variables correlated ($|r| > 0.7$) during the county-level analyses were correlated during the site-level analyses. Therefore, we excluded $Drought_t$, $Drought_{t-1}$, Floristic, and NWI variables, and included $Precip_t$, $Precip_{t-1}$, VegI, and NLCD variables during site-level analyses. In addition to extrinsic variables for trapper effort, multiple models were supported in our site-level model set with all years of available data. However, only one model had greater support compared to the null model, and included Patch Number, suggesting a negative but imprecise relationship with PCHM (Table 2 and Supporting Information S1: Table S10). PCHM was predicted to decrease by 39.00% (95% CL = −62.73–0.46) for each increase of 1 standard deviation in Number of Patches (1422; Figure 3). Our results included no strong effect of effort variables on PCHM as all estimates were imprecise. Similarly, the highest-ranked model for the subset (2011–2018) of site-level data was the null model (Supporting Information S1: Tables S11 and S12). With all additional variables held constant at their respective mean values, the predicted site-level PCHM was 154.74 (95% CL = 89.10–268.73). Effort variables were included in the minimum (null) model, but all estimates were imprecise.

TABLE 2 | Model-selection results of the 10 highest-ranked models within a set of 50 models for analysis of annual site-level harvest data for muskrat (*Ondatra zibethicus*) from six state-managed areas and seven national wildlife refuges within Michigan, Minnesota, and Ohio, USA, during 1996–2018, depending on area. Dependent variable was per-capita harvest of muskrats. Models are ranked based on Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002), where K = number of model parameters, LL = log-likelihood value of model, ΔAIC_c = difference in AIC_c relative to highest-ranked model within the model set, and w = AIC_c weight. Random effects included Site and Harvest Season.

Model	K	LL	ΔAIC_c	w
Number of Patches	8	−235.94	0.00	0.11
Null	7	−237.21	0.36	0.09
Patch Area	8	−236.30	0.72	0.07
Area Emergent Wetlands	8	−236.33	0.79	0.07
Largest Patch	8	−236.36	0.84	0.07
$Precip_{t-1}$	8	−236.61	1.35	0.05
Area Wetlands	8	−236.66	1.45	0.05
Winter Temp	8	−236.80	1.73	0.05
Area Woody Wetlands	8	−236.83	1.79	0.04
Winter Temp + Patch Area	9	−236.09	2.52	0.03

4 | Discussion

Our study is the first to assess both county-level and site-level trends in muskrat population dynamics at the regional scale. Our assessment of these different types of data, including quantifying these relationships, should inform management decisions and recommendations, such as prioritizing specific management actions to mitigate regional declines in muskrats. In addition, given the capacity of muskrats to serve as ecosystem engineers and indicator species in wetland communities (e.g., Bomske and Ahlers 2021), the patterns we uncovered may

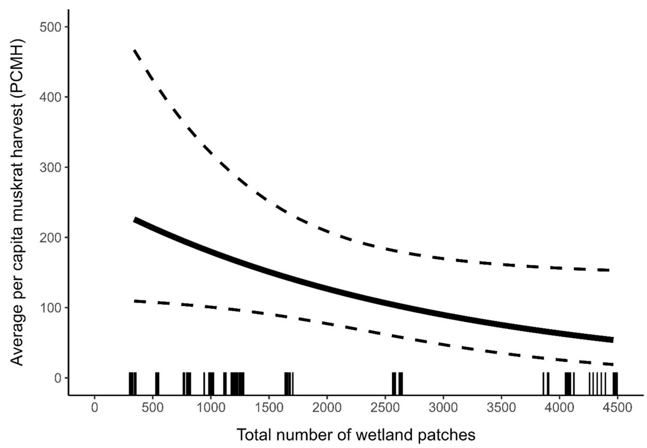

FIGURE 3 | Relationship between annual reported per-capita harvest of muskrats (*Ondatra zibethicus*; PCHM) and the total number of wetland patches based on annual site-level harvest data from six state-managed areas and seven national wildlife refuges in Michigan, Minnesota, Ohio, and Wisconsin, USA, during 2000–2018. Back-transformed relationship (solid lines) and 95% confidence limits (dashed lines) were predicted from the highest-ranking model based on Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) from a model set containing 50 models where all other model variables were held at their mean value. Data included 189 site-harvest season combinations. Distribution of actual values for total number of wetlands patches are shown as a rug plot along the x-axis. Estimates of wetland patches were imprecise (− 0.34; 95% CL = −0.91–0.22).

help guide wetland conservation, restoration, and management within the Midwest.

We found evidence that spatial attributes of wetlands and effects of drought were important drivers of muskrat harvest within the Midwest states. In our county-level analysis, muskrat harvest decreased with increasing distance between wetlands (i.e., reduced connectivity) in the Eastern Temperate Forest and Northern Forest and increased with decreasing connectivity in the Great Plains. However, when considering all three states together, muskrat harvest increased with increasing wetland area in Ohio and the Northern Forest ecoregion of Michigan. Because trapper effort was indirectly (i.e., PCHM) accounted for throughout our modeling efforts, we expect that the relationships between harvest and wetlands is linked to the underlying abundance of muskrats (Ahlers et al. 2016). Our results support the hypothesis that regional-scale declines in abundance of muskrats are likely associated with losses to wetland habitats throughout the Midwest, and more generally, throughout North America.

We found wetter annual conditions were associated with increased muskrat harvest within the Great Plains ecoregion. Although the impacts of drought conditions on wetland ecosystems are complex, reduced water levels and increased distances between areas containing muskrat habitat during drier conditions may lead to decreased reproduction and population sinks (Ahlers et al. 2015; Ward et al. 2021). Furthermore, increases in frequency and duration in high-water levels or flooding events may offer opportunities for muskrat dispersal or displacement, followed by increased reproduction (Ahlers et al. 2015; Straka et al. 2018; Ward et al. 2021). These impacts may be particularly pronounced in the prairie-pothole region where water resources may be limited because of intensive agricultural use (J. Erb, MNDNR, personal communication, 2024). Therefore, in addition to effects of wetland connectivity and size on declining populations of muskrats, our results concur with other studies (i.e., Ahlers et al. 2015; Ward et al. 2021) which suggest climate change may also impact muskrat populations. However, future studies are needed to address direct links between climate change effects and population demographics of muskrats and other wetland-obligate species.

Our analyses may be improved through addressing limitations associated with the availability of important data sets during this study. First, the nationwide effort of the U.S. EPA NWCA program to assess the status and conditions of wetlands throughout our study area is completed every 5 years. Although we were able to incorporate the 2011–2012 and the 2016 data (i.e., variables for Floristic and VegI) from this program in our modeling efforts, no data were available prior to these years, resulting in a small subset of data to test the influence of wetland vegetation on muskrat harvest. If long-term vegetation data were available, including these data may have allowed us to examine relationships between trends in wetland conditions as measured by vegetative index and muskrat harvest, which in turn could enhance our insight into additional factors associated with muskrat population declines.

We acknowledge that site-specific constraints and considerations of political or social conditions at the local or state level may necessarily be integrated into decisions associated with muskrat and wetland management. Under those considerations, increased connectivity and size of wetlands were associated with increased county-level muskrat harvest, indicating that wetland loss has contributed to widespread declines in muskrat populations. Given the role of muskrats as ecosystem engineers in wetland communities, wetland-management actions that increase the abundance and distribution of muskrat populations may synergistically serve to improve wetland function and biodiversity. Although connectivity is an important consideration, creation of a single isolated wetland should not be discouraged despite being less than ideal.

In addition, our efforts to evaluate the utility of using muskrat harvest data as an indicator of wetland condition and to index the population status of other wetland-wildlife species were constrained by too few data that were spatially and temporally consistent within our study area. Identification of wetland areas of interest, particularly those areas where consistent and standardized monitoring efforts to survey populations of other wetland wildlife are or can be established, and where long-term wetland-monitoring programs can also include standardized and relatively comprehensive surveys (e.g., hut-count surveys) for muskrats and wetland characteristics (e.g., vegetation, water quality) should be a priority. Further, for sites with harvest, the collection of harvest data can also be standardized to allow for a much more robust evaluation of muskrat harvest and population trends, and consequently, improved management of both muskrats and wetlands. Efforts to increase and standardize the collection of furbearer harvest data, including to readily facilitate direct comparisons of data sets across jurisdictions, are an important consideration to improve furbearer management (Hiller et al. 2021).

Author Contributions

Tim L. Hiller: conceptualization, funding acquisition, writing – original draft, methodology, validation, writing – review and editing, formal analysis, project administration, supervision, investigation, data curation. **Andrea Sylvia:** formal analysis, writing – review and editing. **Jesse T. Boulerice:** data curation, formal analysis, writing – original draft. **Adam A. Ahlers:** conceptualization, data curation, formal analysis, investigation, methodology, project administration, writing – review and editing, funding acquisition. **Dwayne R. Etter:** conceptualization, investigation, methodology, project administration, writing – review and editing, funding acquisition. **Eric M. Dunton:** conceptualization, investigation, methodology, project administration, writing – review and editing, funding acquisition.

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those of the authors and do not necessarily represent the views of USFWS. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States Government.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Wildlife Ecology Institute Data Repository at https://doi.org/10.59438/BMJV5290.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Supporting File 1: wll270044-sup-0001-SupplementaryFiles_Muskrat1.pdf.