ASSESSING THE VALUE OF AN INDICATOR SPECIES FOR WETLAND QUALITY, CONNECTIVITY, AND WILDLIFE IN THE GREAT LAKES BASIN

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In collaboration with
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ABOUT WILDIFE ECOLOGY INSTITUTE

Wildlife Ecology Institute is a 501(c)(3) tax-exempt organization founded in 2015 and located in Helena, Montana. Our mission is to bridge the research-management disconnect by identifying and utilizing the confluence of applied research, conservation, and education to meet the contemporary challenges of fish and wildlife management. We do this through a teamwork approach by partnering with agencies and other organizations from the project planning stages to project conclusion. This ensures that limited project resources are used wisely and that project products fully address management and conservation needs. Our vision is to lead by example on a journey of building this novel and holistic approach to support fish and wildlife management in an increasingly complex and technical environment. We work throughout the U.S., we have project partners in Canada and Mexico, and our future work may extent to the global scale.

PROJECT SUMMARY

Although muskrats (*Ondatra zibethicus*) provide important ecological, economical, and cultural values to wetland systems in which they occur, populations have been experiencing substantial declines throughout much of North America including throughout the Great Lakes Basin. The cause(s) of these declines are unclear, but may be related to substantial loss and fragmentation of wetland habitat, wetland degradation, impacts from weather or diseases, or other factors. In 2018, we secured funding from the Great Lakes Fish and Wildlife Restoration Act Program to conduct a collaborative project to assess the value of using muskrats as an indicator species for wetland quality, connectivity, and other wildlife throughout the Great Lakes Basin. Along with a goal to evaluate the hypothesis that muskrats serve as an ecological indicator species of wetland quality and the status of other wetland wildlife, we investigated factors influencing regional-scale declines in muskrat populations by evaluating long-term muskrat harvest data. We obtained existing multi-year, multi-scale datasets of muskrat harvest from numerous state and federal wildlife agencies within the Great Lakes Basin. Because the characteristics of data were often spatially or temporally inconsistent, we expanded our analyses to improve our inferences through inclusion of the full spatial extent (when possible) of all U.S. states within the Great Lakes Basin, but without inclusion of those additional efforts in our GLFWRA-funded budget. We evaluated the relationship between muskrat abundance (as indexed by harvest while controlling for trapper effort) and a set of factors that potentially drive muskrat population dynamics. Using generalized linear mixed models and model-selection approaches, we found support that county-level muskrat harvest was positively related to wetland connectivity and wetland area. This suggests that declines in muskrat populations, at least in recent decades, may be related to wetland losses throughout the Great Lakes Basin. Therefore, wetland restoration efforts, especially initiatives that may directly benefit muskrat habitat, may be valuable to the management and conservation of muskrats and other wetland wildlife. We also found that drought conditions influenced harvest, particularly within the Great Plains ecoregion of Minnesota, such that per capita muskrat harvest during abnormally wet conditions was approximately twice that of abnormally dry conditions, as measured by a standardized precipitation index. During analyses of site-level muskrat harvest data from sites within state-managed areas and the National Wildlife Refuge System distributed throughout the Great Lakes Basin, we found that muskrat harvest was negatively associated with higher quality vegetation condition. While this may suggest that muskrat susceptibility to trapping increases in areas where resources are suboptimal, this relationship may also be an artifact of the clustered distribution of study sites with data sufficient for our site-level analysis. We did not find evidence that the richness of secretive marsh birds or waterfowl were associated with per capita muskrat harvest; however, our ability to effectively evaluate this relationship was substantially limited by the paucity of existing site-level datasets with the appropriate spatial and temporal overlap for muskrat and avian populations. Finally, our interpretation of our results also included a positive relationship between muskrat harvest and muskrat abundance (as indexed by annual muskrat hut counts), where 1.9 muskrats were predicted to be harvested annually for every hut counted within a given trapping unit at the Ottawa National Wildlife Refuge, Ohio, USA. Our recommendations include strategies for managers throughout the Great Lakes Basin to increase the value of data collected during annual furharvester surveys to more effectively monitor muskrats and factors affecting their populations.

INTRODUCTION

Despite providing valuable habitat to a host of wildlife species and critical ecosystem services to the surrounding environment (Costanza et al. 1997, Zedler and Kercher 2005), wetlands loss across the U.S. has been substantial, including throughout the Great Lakes Basin (Dahl and Allord 1996, Mitch and Gosselink 2007). At the national scale, >53% of wetland habitat has been lost since the late 18th Century (Dahl and Allord 1996, Mitch and Gosselink 2007). Approximately 50% of wetlands have been destroyed in Michigan and Minnesota, whereas >1.5 million ha (3.4 million acres) of wetlands in Ohio have been converted to other uses (Dahl 1990, Dahl and Allord 1996). The 2012 results of the National Wetland Condition Assessment (NWCA), which was conducted by the U.S. Environmental Protection Agency (U.S. EPA) to identify, categorize, and examine stressors to wetlands based on plant community and water quality conditions, concluded that an estimated 32% of wetlands in the U.S and 19% of wetlands with the Great Lakes Basin were experiencing high levels of stress from invasive vegetative species (U.S. EPA 2016). Linking the impacts of these losses and stressors to the status and quality of wetlands to wildlife populations has rarely occurred at the regional level. A regional examination of these impacts to wildlife may reveal patterns not apparent at smaller spatial scales, thereby allowing conservationists and managers to direct informed actions on addressing large-scale wetland issues.

Muskrats are important wetland-obligate species that may represent an ecosystem engineer and an indicator of ecosystem health in wetland communities (Higgins and Mitsch 2001, Bomske and Ahlers 2021). For example, although cattail species are a natural component of wetland succession, both native species (e.g., *Typha latifolia*), and hybrid species (*Typha* × *glauca*) can result in monocultures that reduce habitat heterogeneity and biodiversity in wetland communities (Martin et al. 1957, Patton 1975, Toner 2006). When abundant, muskrats can setback growth of wetland vegetation, including cattails, through intense herbivory (Smirnov and Tretyakov 1998, Clark 2000, Erb and Perry 2003, Nummi et al. 2006, Kua et al. 2020). Herbivory by muskrats may serve to improve quality, function, and biodiversity of wetlands used by other wetland wildlife, such as waterfowl, marsh birds, amphibians, fish, and invertebrates (Kaminski and Prince 1981, Nelson and Kadlec 1984, de Szalay and Cassidy 2001, Nummi et al. 2006). As a result of these processes, increased muskrat abundances may positively affect wetland function, and therefore indicative of local or regional ecosystem health in wetland communities.

Muskrats may also be an indicator species other wetland-obligate species, particularly avian species. The hemi-marsh conditions created and maintained by muskrats through intense herbivory creates a mix of open water and vegetative structure, can provide nesting and loafing areas for migrating waterfowl and waterbirds. For example, the diversity of dabbling ducks was greater in wetlands experimentally managed to mimic hemi-marsh conditions that typically occur because of abundant muskrat populations, as compared to less structurally diverse wetland conditions (Kaminski and Prince 1981). Similarly, muskrat-related structures (e.g., huts and feeding platforms) served as the dominant nesting substrate for black terns (*Chlidonias niger*), a migratory bird of conservation concern (Hickey and Malecki 1997, U.S. Fish and Wildlife Service [USFWS] 2008). These examples suggest that determining if and how information on muskrat populations can be used to infer the status of waterbirds as an indicator species could be valuable to waterfowl and wetland management.

Wildlife professionals and trappers have expressed concerns that muskrat populations throughout much of North America have declined substantially. Recent empirical evidence echoes these concerns that declines in muskrat populations are widespread in distribution and long term in duration, including within the Great Lakes Basin (Toner 2006, Ahlers and Heske 2017, Ward and Gorelink 2018, Sadowski and Bowman 2021). Population declines could reflect larger issues in aquatic systems that may negatively impact other wetland wildlife, including those that benefit directly or indirectly from muskrat activities (e.g., American mink [*Neovison vison*], waterfowl, waterbirds, amphibians, turtles and other reptiles, fish, insects; Erb and Perry 2003, Wilcox and Xie 2008). In addition, along with North American beavers (*Castor canadensis*) and northern raccoons (*Procyon lotor*), muskrats are considered the current backbone of the international wild fur trade (Novak et al. 1987, Association of Fish and Wildlife Agencies 2017). During the past 40 years (1974–2014), an estimated minimum of 128 million muskrats were harvested in the U.S., making this species an important contributor to both the economic and cultural components of the fur trade (Association of Fish and Wildlife Agencies 2017).

Although mechanistic explanations for muskrat population declines are unknown, some hypotheses exist that may explain observed declines (Ahlers and Heske 2017). For instance, historic and continued loss of wetlands and declines in wetland quality, such as those experienced throughout the Great Lakes Basin, have likely negatively affected muskrats and other wetland wildlife species by altering wetland vegetation dynamics, reducing population connectivity, and limiting the availability of high-quality habitat (Clark 2000, Erb and Perry 2003, Ervin 2011, Ward and Gorelink 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 (Bellrose et al. 1943, Piha et al. 2007, Ahlers et al. 2015), which have 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). Increased exposure to contaminants in degraded wetlands may also reduce muskrat survival and reproduction (Ohio Department of Natural Resources [ODNR] 2016). No single factor has been identified, however, as the driver of muskrat population declines, and little information exists as to how the impact of these factors may vary spatially across the large distribution of muskrats in the Great Lakes Basin.

Harvest data often represent the only long-term and geographically widespread datasets for many furbearing species, including muskrats (White et al. 2015, Ahlers et al. 2016). Inherently, harvest is linked to local or regional abundances of species (McKelvey et al. 2011, Ahlers et al. 2016). Therefore, harvest data represent a valuable tool to assess population trends (Ahlers and Heske 2017; Hiller et al. 2018, 2021). For muskrats, harvest data may serve as resource for evaluating causes of muskrat declines where data can be appropriately linked to factors expected to impact muskrat populations dynamics, including wetland loss and degradation, weather patterns, pollutants, or disease. Similarly, given the potential link between muskrat abundance, wetland function, and other wetland wildlife, muskrat harvest data may represent a valuable management tool for assessing the status of wetland ecosystems. However, when using harvest data to guide research and management of furbearing species, the potential influence of trapper effort must be considered to ensure biological factors that influence species abundance are disentangled from factors influencing trapper effort (Landholt and Genoway 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). Similarly, efforts to increase and standardize collection of furbearer harvest data, including to readily facilitate direct comparisons of datasets across jurisdictions, is an important consideration to improve furbearer management (Hiller et al. 2021).

We conducted a regional evaluation of the relationship between muskrat abundance, as indexed by muskrat harvest data, and a set of factors potentially associated with muskrat population dynamics through analysis of a series of multi-year and multi-spatial-scale datasets documenting annual muskrat harvest collected throughout the Great Lakes Basin. First, we evaluated if muskrat harvest data obtained by state and federal agencies could be used to evaluate relationships between annual muskrat harvest and variables related to wetland condition, quality, and spatial attributes, along with weather, landcover types, and other factors. We used two spatial scales for our analyses, including 1) county-level harvest obtained from statewide furharvester surveys, and 2) site-level harvest data obtained from sites within state-managed areas and the National Wildlife Refuge System throughout the Great Lakes Basin. At both scales, we assessed whether existing harvest data may be used to infer population-level effects on abundance of muskrats, and we investigated factors associated with apparent muskrats declines in the Great Lakes Basin. We hypothesized that factors associated with wetland condition, area, and connectivity (i.e., distance between wetlands) would be important contributors to annual population abundance (as indexed by annual harvest) given that muskrats are wetland obligates and wetland habitat has experienced substantial declines in spatial extent and condition throughout the Great Lakes Basin. Second, we evaluated the utility of using site-level harvest data as an index of the population status and trends of other wetland wildlife species, including secretive marsh birds and waterfowl. We predicted that if muskrat abundance could be disentangled from trapper effort, annual harvest data would be positively correlated with measures of population status for these avian species. Finally, we evaluated the relationship between muskrat harvest and muskrat population status as indexed by muskrat hut-count surveys at the scale of a trapping unit within Ottawa National Wildlife Refuge (Ottawa NWR). We hypothesized that if harvest data were representative of the underlining local abundance of muskrat populations, the annual number of muskrats harvested would be positively correlated with annual hut counts. An assessment of these different types of harvest data, including quantifying these relationships, should inform management decisions and recommendations, such as and 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, quantifying these relationships may help guide wetland conservation, restoration, and management within the Great Lakes Basin.

Our objectives of this project were to:

1. Coordinate with state and federal agencies, universities, and NGOs within areas of Great Lakes states (e.g., IL, MI, MN, OH) that lie within the Great Lakes Basin to compile datasets of long-term muskrat relative abundance (e.g., state trapper surveys),

wetland quality (e.g., EPA National Wetland Condition Assessment), and additional sensitive wetland wildlife species (e.g., Midwest Coordinated Bird Monitoring Partnership).
2. Develop models to test the reliability of using muskrats as an indicator species for wetland quality, and dependent on availability of pre-existing data, as a surrogate for monitoring rare and difficult-to-observe species.
3. Develop models to test the relationship between waterfowl use of wetlands and muskrat abundance indices to assess effects of muskrats on waterfowl.
4. Based on results, make recommendations to implement a consistent Great Lakes Basin monitoring program for muskrats to assess wetland quality and range-wide population declines of muskrats and describe how this monitoring program will benefit other wetland wildlife species.

Prior to implementing objectives 2–4, we achieved objective 1 through extensive and comprehensive correspondence and partnerships with multiple agencies and organizations; the data obtained are fully described in several sections of our report. For objectives 2 and 3, we fully document below development of several model sets, the results of those modeling efforts, and our interpretation of those results. Finally, for objective 4, we provide several recommendations associated with interpretation of our results such that these may directly inform decision-making and benefit muskrat and wetland management and conservation.

STUDY AREA

We defined our study based on the spatial extent of the muskrat harvest data collected during 2000–2018 (Fig. 1). The Great Lakes Basin comprises an area >765,000km^2, 17,000 km of shoreline along each of the five Great Lakes in the U.S. and Canada, and includes all or portions of eight U.S. states (Danz et al. 2007; Fig. 1). In the U.S., the Great Lakes Basin is characterized primarily by two broad ecoregions (as defined by the U.S. EPA Level I ecoregion classification system): the Eastern Temperate Forest and the Northern Forest (Omernik and Griffith 2014). The Northern Forest has relatively dense forested areas and sparse populations of humans, whereas the Eastern Temperate Forest has relatively greater agricultural use and higher population densities of humans (Danz et al. 2007). We expanded our study area to also include all of Minnesota and Ohio, including those areas not within the Great Lakes Basin. This resulted in inclusion of the Great Plains ecoregion within Minnesota; this ecoregion consists of primarily agricultural land use, has relatively flat, dry terrain, and was historically grasslands (Omernik and Griffith 2014). In addition to our data analysis across the entire study area, we conducted a site-level analysis that included 13 sites within state-managed areas and the National Wildlife Refuge System throughout the Great Lakes Basin (Fig. 2). These sites varied in area from 18.9 to 481.2 km^2; 12 sites were located in the Eastern Temperate Forest, one site in the Northern Forest, and zero sites in the Great Plains. Lastly, we conducted an analysis specific to Ottawa National Wildlife Refuge (Ottawa NWR), Ohio, USA, using a comprehensive data set collected during 2001–2018. The Ottawa NWR is located in Ottawa and Sandusky counties in northern Ohio and along the southern shoreline of Lake Erie (Fig. 2). The refuge consists of 26 km^2 of diked wetlands managed primarily for moist-soil vegetation and marsh conditions (Cowardin et al. 1979). The vegetation community at the Ottawa NWR includes species such as chufa (*Cyperus* *esculentus*), Walter's millet (*Echinochloa walteri*), rice cutgrass (*Leersia oryzoides*), nodding smartweed (*Polygonum lapathifolium*), pickerel weed (*Pontederia cordata*), common arrowhead (*Sagittaria latifolia*), softstem bulrush (*Scirpus validus*), and narrowleaf cattail (*Typha angustifolia*; Robb et al. 2001).

METHODS

Harvest Data

We requested muskrat harvest information from state and federal biologists responsible for managing furbearer populations within our study area. For our county-level analyses, we obtained data from Michigan Department of Natural Resources (MIDNR), Minnesota Department of Natural Resources (MNDNR), and ODNR. Each of these agencies implemented state-specific protocols for collecting information on furbearer harvest from trappers. Each agency used furharvester surveys mailed to a subset of licensed trappers, responses were voluntary, and data were collected at the county level. The specific questions asked of trappers related to trapper effort varied by state (Table 1). For our site-level analyses, we compiled a series of datasets detailing annual muskrat harvest collected at 18 state-managed areas and 8 national wildlife refuges in Indiana, Michigan, Minnesota, Ohio, and Wisconsin provided by various state and federal wildlife agencies. Methods for collecting data on harvest from muskrat trappers 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) also varied by site. For each site, we consulted with site managers about collection methods, and data quality and limitations. Based on these discussions, we included datasets only from sites 1) where number of trappers per year could be quantified and assigned to the corresponding annual harvest data, 2) with >5 seasons of data on muskrat harvest, and 3) where the date range of harvest data was 2000–2018 (Table 2, Fig. 2). We summarized all site-level datasets reviewed but excluded from analyses and described our rationale for exclusion (Table 3). For our analyses specific to the Ottawa NWR, we obtained harvest data from the USFWS. USFWS collected annual muskrat harvest data via mandatory reporting required by all permitted trappers at the Ottawa NWR from 2001–2018 (USFWS, unpublished data). Each trapper was required to report the total number of muskrats harvested within their assigned trapping unit following the completion of the muskrat harvest season.

Factors Influencing County-Level Harvest

Our ability to directly quantify trapper effort specifically attributable to muskrat harvest differed based on the specific questions asked within furharvester surveys conducted by each state agency (Table 1). For example, although information on number of traps set specifically for muskrats was available for Minnesota and Ohio, these data were not requested of trappers in Michigan. Therefore, we conducted multiple analyses with the goal of 1) assessing regional muskrat harvest across multiple states based on a common index for harvest (i.e., per capita muskrat harvest), and 2) assessing state-specific muskrat harvest based on the best available index for quantifying trapper effort for each state (i.e., muskrat catch-per-trap-day for Minnesota and Ohio, muskrat catch-per-day for Michigan).

In our analysis of regional per capita muskrat harvest, we combined data from each of the 3 states into a single dataset. We defined our dependent variable of per capita muskrat harvest (PCMH) for each county and harvest season as:

$$\text{PCMH} = \frac{\sum Harvest_i}{\sum Trappers},$$

where $Harvest_i$ = number of muskrats reported as harvested by an individual trapper (i), and *Trappers* = number of trappers reporting muskrat harvest.

Annual furharvester surveys conducted in Minnesota and Ohio included data on trapper effort by specifically requesting county-level information on total number of days spent trapping for muskrats and mean number of traps set per day for muskrats. We used these data to define our dependent variable for muskrat harvest in Minnesota and Ohio as muskrat catch-per-trap-day (CPTD) for each county and harvest season as:

$$\text{CPTD} = \frac{\sum Harvest_i}{\sum (Traps_i \times Days_i)},$$

where $Harvest_i$ = number of muskrats reported as harvested by an individual trapper (i), $Traps_i$ = number of traps set per day by an individual trapper (i), and $Days_i$ = number of days spent trapping by an individual trapper (i).

Annual furharvester surveys from Michigan included data on trapper effort by specifically requesting county-level information on total number of days spent trapping for muskrats. However, number of traps set for muskrats was not included. Therefore, in our analysis of state-specific muskrat harvest, we defined our dependent variable for muskrat harvest in Michigan as muskrat catch-per-day (CPD) for each county and harvest season as:

$$\text{CPD} = \frac{\sum Harvest_i}{\sum Days_i},$$

where $Harvest_i$ = number of muskrats reported as harvested by an individual trapper (i), and $Days_i$ = number of days spent trapping by an individual trapper (i).

In all cases, we excluded any data when calculating PCMH, CPTD, or CPD from surveys that contain errors, such as an individual trapper that reported number of days greater than available in a given harvest season, grammatical errors that affected interpretation of data, or otherwise incomplete data. For any survey responses in which multiple counties were listed for muskrat harvest, we divided values equally by counties listed.

To test our hypotheses related to factors influencing population dynamics of muskrats, we included existing data collected within our study area by several sources. We used only data that we considered to be biologically meaningful in relation to the county-level scale of the harvest data, and otherwise of sufficient temporal and spatial completeness (Tables 4 and 5).

We developed a set of county-level variables associated with annual weather patterns to evaluate the influences of temperature, precipitation, and drought indices on muskrat harvest and population dynamics (Table 4). 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 ($PDSI_t$, SPI_t, respectively), and for the preceding year ($PDSI_{t-1}$, SPI_{t-1}). Data for PDSI and SPI were obtained from gridded datasets of surface meteorological variables (gridMET dataset; Abatzoglou 2013) and were extracted for each county using Climate Engine, a derivative and dependency of Google Earth Engine (Huntington et al. 2017).

We defined a set of variables to quantify landscape-scale landcover and spatial attributes of wetlands associated with each county (Table 4). Using the landcover classes within the National Land Cover Database (NLCD) program (Multi-Resolution Land Characteristics Consortium 2021), we estimated the total area (%) of each of the 3 landcover classes (open water, woody wetland, and emergent herbaceous wetland) associated with wetlands within each county for each of the seven years (2001, 2003, 2006, 2008, 2011, 2013, and 2016) in which the NLCD program was conducted during our study. We also combined a subset of existing landcover classes to create 3 additional categories to define broader-scale landcover types that may affect muskrat population dynamics, 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 average area of all wetland patches (Patch Area), largest area of a wetland patch (Largest Patch), average Euclidian 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. 4.0.3 (R Core Team 2021). We defined individual patch size as a single raster cell based on the spatial resolution (30 m) of NLCD. For all landcover 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 dataset. Finally, we assigned each county to one of the 3 ecoregions (Eastern Temperate Forest, Great Plains, and Northern Forest) within our study (Omernik and Griffith 2014). For any counties that included >1 ecoregion, we assigned the ecoregion with the greatest area (%) within that county (Fig. 1).

To evaluate the effects of wetland vegetation on muskrat harvest and population dynamics, we interpolated variables for floristic quality index (FQI) and vegetative multimetric index (VMMI; Magee et al. 2019) based on data derived from 3 wetland assessment and monitoring programs conducted within our study area. These programs included the National Wetland Condition Assessment (NWCA) conducted by U.S. EPA (2016), 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 depending on location and data source. We used kriging interpolation to create predictive contours for both FQI and VMMI for our study area using the gstat package (Pebesma 2004, Graler et al. 2016) in Program R. We then assigned FQI and VMMI values to each county based on the average value of the predicted contours within each county. For data collected by NWCA and ORAM, FQI and VMMI were available only for a single year (either 2011 or 2012) during our study period. Therefore, we used a constant value for FQI and for VMMI for all years of our study. For both FQI and VMMI, vegetation condition of wetlands was considered to more representative of native, undisturbed, plant communities at higher values compared to non-native, disturbed communities at lower values (U.S. EPA 2016, Magee et al. 2019).

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

We used generalized linear mixed modeling (GLMM) to evaluate the relationship between each respective index of muskrat harvest (i.e., regional PCMH [all States], CPTD [MN, OH], CPD [MI]) and our set of independent variables associated with each analysis. To avoid autocorrelation potentially affecting our modeling approach, we used the Pearson product-moment correlation coefficient (r) and did not include both variables in the same model for any pair of variables that were highly correlated ($|r|>0.7$; Sheskin 2007). We transformed our dependent variables using a natural-log transformation and rescaled all of our independent variables by centering and dividing by one standard deviation to aid model convergence and interpretation (Schielzeth 2010). In all models in each model set, we included the 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. For our regional analysis of PCMH, we included extrinsic variables related specifically to trapper effort (i.e., pelt price, unemployment, and gas price) in all models within this model set. We assessed the fit of our model sets by visual examination of the residuals from a global model for indication of systematic lack of fit. 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). We performed all statistical analyses using Program R.

Factors Influencing Site-Level Harvest

We expected many of the same variables described above for assessing county-level muskrat harvest would potentially influence site-level harvest. Therefore, we used the same set of variables described above for all site-level analyses, but adjusted the spatial scale to more appropriately represent the scale of our 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 the boundaries of the site (i.e., annual PDSI and SPI). For those variables associated with landcover 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 annual pelt price, unemployment rate, and gas price, we used state-level values.

Because only 2 of the site-level muskrat harvest datasets directly quantified trapper effort, we used per capita muskrat harvest (PCMH) while controlling for extrinsic factors influencing trapper effort as our dependent variables to standardize comparisons across sites. We used GLMM to evaluate the relationship between PCMH and the set of independent variables for each site. To avoid autocorrelation within models, we did not include variables in the same model for any pair of variables that were highly correlated ($|r|>0.7$; Sheskin 2007). We transformed PCMH using a natural-log transformation and rescaled all of our independent variables by centering and dividing by one standard deviation to aid model convergence and interpretation (Schielzeth 2010). In all models in 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 a null model. Similar to our regional analysis of PCMH, we included effects of pelt price, unemployment, and gas price in all models to account for trapper effort. We assessed model fit by visual examination of the residuals from a global model for indication of systematic lack of fit. We used AIC_c to rank models based on model complexity and fit (Burnham and Anderson 2002). We performed all statistical analyses using Program R.

Influence of Muskrats on Other Wetland Wildlife

We evaluated the relationship between abundance of muskrats (indexed by harvest) and population characteristics of other wetland wildlife species for state-managed areas and sites within the National Wildlife Refuge System with sufficient data. In particular, we quantified relationships between richness of secretive marsh birds and waterfowl with PCMH, while accounting for additional variables expected to influence avian populations, to test the reliability of using muskrats as an indicator species in wetland systems.

We calculated dependent variables for annual richness of at 8 sites for secretive marsh birds (SMBs) and 6 sites for waterfowl (Table 2). We derived our calculation of SMB richness from data collected at each site as part of annual SMB surveys conducted by Michigan State University (M. Monfils, Michigan State University, unpublished data), ODNR (L. Kearns, ODNR, unpublished data), MNDNR (S. Saunders, National Audubon Society, unpublished data), and USFWS. SMB surveys were conducted using the national protocol for inventory and monitoring SMBs (Conway 2015). Our calculation of waterfowl richness was derived by combining two survey protocols. For state-managed areas (n = 5), waterfowl surveys were completed using ground surveys on designated routes. All 5 of the state-managed areas with datasets on waterfowl occurred in Michigan where waterfowl surveys were completed by MIDNR (MIDNR, unpublished data). For NWRs (n = 2), waterfowl surveys were conducted following the national protocol for inventorying and monitoring nonbreeding waterbirds (Intergraded Waterbird Management and Monitoring; Loges et al. 2021). For both state and federal sites, we calculated annual richness as the number of unique species detected during a given year and during all surveys conducted within the boundaries of each site. We assigned year of survey to the corresponding year in which a harvest season for muskrats was initiated.

We used GLMM to evaluate the relationship between richness of SMBs or waterfowl and all of our independent variables available for each site, including PCMH. To avoid autocorrelation within models, we did not include variables in the same model for any pair of variables that were highly correlated ($|r|>0.7$; Sheskin 2007). We rescaled all of our independent variables by centering and dividing by one standard deviation to aid model convergence and interpretation (Schielzeth 2010). Because our dependent variables for richness represented count-based data, we evaluated our models using the Poisson distribution. For all models in both model sets, we included the categorical variables site and harvest season as random effects. To determine if muskrat harvest, as measured by PCMH, was influential to SMB and waterfowl richness, we compared models with and without PCMH as an independent variable. We first constructed a partial set of *a priori* models by logically grouping all variables except for PCMH. We then constructed the remaining models for each set by creating a new model for every model in the partial set that also included PCMH. To control for the influence of sampling effects when calculating both waterfowl and SMB richness, we included variables quantifying the area (km^2) of each site (i.e., sample area), total number of surveys conducted within a given year (i.e., number of samples), and total count of all individual birds detected during all surveys (i.e., number of individuals) as independent variables in all models (Dunn et al. 2009, Gotelli and Colwell 2011). Each of our model sets also included a null model. We assessed model fit by estimating the variance inflation factor ($\hat{c}$) based on the chi-square goodness-of-fit test and visual examination of the residuals from a global model for indication of systematic lack of fit. We used AIC_c to rank models based on model complexity and fit (Burnham and Anderson 2002). We performed all statistical analyses using Program R.

Relationship between Muskrat Harvest and Muskrat Abundance

In addition to harvest data, USFWS conducted muskrat hut count surveys each year for all wetlands within the Ottawa NWR from 2001–2018 (USFWS, unpublished data). These surveys are completed in late October to early November when detection of muskrat huts is greatest. The entire perimeter of every wetland was driven each year with periodic stops where visual counts of all huts were completed. From this dataset, we created an independent variable for annual muskrat hut count per trapping unit by summing the hut count values of all wetland units within each trapping unit annually.

Based on harvest data obtained from USFWS, we developed a dependent variable for muskrat harvest defined as the total annual muskrat harvest per trapping unit at the Ottawa NWR over the 17-year period from 2001–2018. We used GLMM to evaluate the relationship between annual muskrat harvest and muskrat hut counts at the Ottawa NWR. We compared one model including our independent variable for hut count to a second model without the hut count variable. We included extrinsic variables of pelt price, unemployment, and gas price in all models to account for trapper effort. We included terms for trapping unit and harvest season as random effects in both models. We used AIC_c to rank models based on model complexity and fit (Burnham and Anderson 2002). We performed all statistical analyses using Program R.

RESULTS

Harvest Data

Our regional analysis of county-level muskrat harvest consisted of data obtained from 258 counties within 3 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 (Table 6). After filtering those datasets that did not meet our inclusion parameters described above, our site-level analyses contained harvest data from 6 state-managed areas and 7 national wildlife refuges (Table 2, Fig. 2). Throughout these 13 sites, a combined total of 324,245 harvested muskrats were reported by 1,339 trappers. Date ranges of site-level data on muskrat harvest included in our model set varied by site (Table 2). Based on USFWS harvest data, the total reported harvest of muskrats at the Ottawa NWR during 2001–2017 was 62,327, with an annual average of 3,666 muskrats harvested. These data were obtained from 124 trapping units with an average of 7.3 units trapped per year.

Factors Influencing County-Level Harvest

Several of our independent variables were correlated including SPI_t and $PDSI_t$ ($r = 0.87$), $SPI_{t\text{-}1}$ and $PDSI_{t\text{-}1}$ ($r = 0.87$), FQI and VMMI ($r = 0.77$), and many of our variables assessing wetland distribution based on NLCD with those based on NWI ($r > 0.7$). Because each pair of correlated variables represented variables quantifying the same underlying attribute, we removed one variable in each pair from further analysis to reduce redundancy and to aid model interpretation. Specifically, we removed $PDSI_t$, $PDSI_{t\text{-}1}$, FQI, and NWI variables from consideration, while SPI_t, $SPI_{t\text{-}1}$, VMMI, and NLCD variables remained.

Our highest-ranked model from our regional model set (AIC_c weight [w]= 0.60; Table 7, model 1) contained pairwise interactions between Connectivity, SPI_t, and $SPI_{t\text{-}1}$ with Ecoregion. This model suggested PCMH was negatively related to distance (m) between wetland patches (β = −0.28, SE = 0.12, 95% CI = −0.53 to −0.03), positively related to SPI_t (β = 0.05, SE = 0.02, 95% CI = 0.02 to 0.08) and $SPI_{t\text{-}1}$ (β = 0.07, SE = 0.01, 95% CI = 0.04 to 0.10), whereby the intercept and strength of each relationship varied by Ecoregion (Figs. 3–5). Compared to the Great Plains ecoregion (*Intercept*; β = 2.85, SE = 0.10, 95% CI = 2.64 to 3.05), this model suggested PCMH was 23% lower in the Northern Forest ecoregion (β = −0.66, SE = 0.16, 95% CI = −0.97 to −0.34), but similar in the Eastern Temperate Forest ecoregion (β = 0.00, SE = 0.05, 95% CI = −0.11 to 0.11).

Based on annual furharvester surveys in Minnesota, the annual average CPTD for all counties was 0.12 (SD = 0.03) muskrats per trap-day. Our most-supported model (w = 0.55; Table 8, model 1) suggested a positive relationship with CPTD and our independent variables for SPI_t (β = 0.20, SE = 0.04, 95% CI = 0.12 to 0.27) and SPI_{t-1} (β = 0.10, SE = 0.04, 95% CI = 0.03 to 0.17). Based on this model, CPTD was predicted to double (0.05 to 0.1) when SPI_t values indicated moderately dry conditions (SPI_t = −1.5) compared to when SPI_t values indicated moderately wet conditions (SPI_t = 1.5; Fig. 6). The second-ranked model (w = 0.28, ΔAIC_c = 1.33; Table 8, model 2) suggested a positive relationship with CPTD and our independent variables for SPI_t (β = 0.20, SE = 0.04, 95% CI = 0.12 to 0.27), and SPI_{t-1} (β = 0.10, SE = 0.04, 95% CI = 0.03 to 0.17), and a slightly negative relationship between CPTD and Connectivity with confidence intervals that overlapped zero (β = −0.05, SE = 0.06, 95% CI = −0.17 to 0.07).

Based on annual furharvester surveys in Ohio, the annual average CPTD for all counties was 0.09 (SD = 0.03) muskrats per trap-day. Our most-supported model (w = 0.34; Table 9, model 1) suggested a positive relationship with CPTD and our independent variable for Area Emergent Wetlands (β = 0.12, SE = 0.04, 95% CI = 0.02 to 0.04), but a negative relationship between CPTD and Connectivity with confidence intervals that overlapped zero (β = −0.08, SE = 0.04, 95% CI = −0.15 to 0.01). Based on this model, CPTD is predicted to increase 2-fold, from 0.06 to 0.13 muskrats per trap-day, as area of emergent herbaceous wetlands increases from 1% to 10% when Connectivity is held at the mean value (Fig. 7). This model also predicts that CPTD will decrease from 0.075 to 0.05 (33.3%) as distance (m) between wetland patches increases from 100 m to 700 m when Area Emergent Wetlands is held at the mean value (Fig. 8). The top 4 models in this model set all contained the independent variable for Area Emergent Wetlands (Σw = 0.83, Table 9). For each of these models, the estimated relationship between PCMH and Area Emergent Wetlands was similar to the relationship predicted by our top model (β ± 0.03).

Based on annual furharvester surveys in Michigan, the annual average CPD for all counties was 1.7 (SD = 0.03) muskrats per day spent trapping. In addition to extrinsic variables for trapper effort, our most-supported model (w = 0.50; Table 10, model 1) contained our variable for Largest Patch and a pairwise interaction between Area Wetlands and Ecoregion. This model suggested a positive relationship between CPD and largest area (km^2) of wetland patch (β = 0.17, SE = 0.06, 95% CI = 0.05 to 0.28), and CPD was predicted to be lower in the Northern Ecoregion (β = −0.22, SE = 0.06, 95% CI = −0.34 to −0.09) compared to the Eastern Temperate Forest (*Intercept*; β = 0.00, SE = 0.06, 95% CI = −0.14 to 0.13; Fig. 9). The relationship between CPD and Area Wetlands varied by Ecoregion (Fig. 10).

Factors Influencing Site-Level Harvest

As in the county-level analysis described above, we found the same pairs of variables to be correlated ($|r|$ >0.7) in our site-level analyses. Therefore, we removed $PDSI_t$, $PDSI_{t-1}$, FQI, and NWI variables from consideration, while SPI_t, SPI_{t-1}, VMMI, and NLCD variables remained. In addition to extrinsic variables for trapper effort, our highest-ranked model from our site-level model set (w = 0.28; Table 11, model 1) contained our independent variable for VMMI and suggested a negative relationship between PCMH and VMMI (β = −0.69, SE = 0.23, 95% CI = −1.12 to −0.27; Fig. 11). Based on this model, PCMH was predicted to decrease from 390 to 170 muskrats harvested per trapper as VMMI increased from 42 to 53 units. The top 7 models in this model set all contained the independent variable for VMMI ($\Sigma w = 0.63$, Table 11). For each of these models, the estimated relationship between PCMH and VMMI was similar to the relationship predicted by our top model ($\beta \pm 0.09$).

Influence of Muskrats on Other Wetland Wildlife

Our evaluation of the relationship between SMB richness and PCMH included data from 8 sites in 4 states (Table 2). Our highest-ranked model that included the independent variable for PCMH was the 10th-ranked model in our set for SMB richness ($w = 0.02$, $\Delta AIC_c = 2.66$; Table 12, model 10). This model suggested a slightly negative relationship between SMB richness and PCHM with 95% confidence intervals that overlapped zero ($\beta = -0.03$, SE = 0.08, 95% CI = −0.21 to 0.11) when all other independent variables were held at their respective mean values. Our evaluation of the relationship between waterfowl richness and PCMH included data from 6 sites occurring in 2 states (Table 2). Our highest-ranked model that included the independent variable for PCMH was also the 10th-ranked model in our model set for waterfowl richness ($w = 0.03$, $\Delta AIC_c = 2.86$; Table 13, model 10). This model suggested a slightly positive relationship, though modest, between waterfowl richness and PCHM with 95% confidence intervals that overlapped zero ($\beta = 0.02$, SE = 0.06, 95% CI = −0.09 to 0.14) when all other independent variables were held at their respective mean values.

Relationship between Muskrat Harvest and Muskrat Abundance

In our evaluation of harvest and abundance at Ottawa NWR, our model containing hut counts had a better fit to the data based on AIC_c than our competing model without the variable for hut count (log likelihood of −875.04 versus −900.78, $w = 0.99$ versus <0.01). This model suggested a positive relationship between harvest and hut count ($\beta = 237.97$, SE = 32.43, 95% CI = 172.23 to 306.41), which predicted an increase of 1.9 muskrats harvested for each additional hut observed within a trapping unit (Fig. 12).

CONCLUSIONS

Using long-term data on muskrat harvest, we found evidence that spatial attributes of wetland habitats and drought conditions were important drivers of muskrat harvest within the Great Lakes Basin and associated states. In our county-level analysis, muskrat harvest decreased with increasing distance between wetlands (i.e., reduced connectivity) when considering all three states together, and also increased with increasing wetland area in Ohio and the Northern Forest ecoregion of Michigan. Because trapper effort was either directly (i.e., CPTD or CPD) or indirectly (i.e., PCHM) accounted for throughout our modeling effort, we expect that these relationships between harvest and wetlands are 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 the losses to wetland habitats throughout the Great Lakes Basin, and more generally, throughout North America. We also found wetter conditions resulted in increased muskrat harvest within the Great Plains ecoregion. While the impacts of drought conditions on wetland ecosystems are complex, reduced water levels and increased distances between muskrat habitats during drier conditions may lead to decreased reproduction and population sinks (Ahlers et al. 2015, Ward et al. 2021), while 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 potholes region where water resources may be limited because of intensive agricultural use (J. Erb, MNDNR, personal communication). Therefore, in addition to the role of wetland connectivity and area on declines in muskrats, our results add to other studies (i.e., Ahlers et al. 2015, Ward et al. 2021) which suggest climate change may also impact muskrat populations.

Within the 13 sites considered in our analyses, and within the constraints of our data, muskrat harvest was negatively related to site-level vegetation condition. This finding contradicts the hypothesis that sites with higher vegetative quality would harbor greater abundances of muskrats, which putatively should be indexed by greater muskrat harvest. We postulate that this unexpected result may be an artifact of the limited spatial distribution of sites with sufficient muskrat harvest data that we could include in our analyses. Notably, several sites were spatially clumped (i.e., 61% of sites were located in either southeastern Michigan or northcentral Ohio) and the range of interpolated values of VMMI for sites represented only a portion of the range of values possible for the Great Lakes Basin (i.e., range of 42.5 to 52.0 versus 9.6 to 82.5, respectively). For example, we were unable to obtain suitable site-level muskrat harvest data from any location within those portions of northeastern Minnesota and the Upper Peninsula of Michigan, which are areas generally classified as the highest VMMI values in the Great Lakes Basin. Therefore, our derived relationship between muskrat harvest and wetland vegetation condition may not be representative of the entire Great Lakes Basin. Alternatively, this inverse relationship between harvest and vegetation condition could be influenced by confounding variables which we were unable to include for in our analyses, such as water levels, pollutants, and factors effecting muskrat catchability. In any case, further research evaluating the impact of varying levels of vegetation condition on muskrat populations would be informative, and this would need to include a wider distribution of sites within the Great Lakes Basin and a wider range of values for VMMI.

We did not find a relationship between muskrat harvest and wetland use of either SMBs or waterfowl populations at the site-level scale. This result could suggest that muskrats, or our index of muskrat abundance, may not be a valuable indicator for habitat quality for wetland fauna, at least for those avian species evaluated herein. However, we note that our ability to evaluate this relationship was hindered by the lack of available data on SMB and waterfowl populations within wetland habitats where muskrat harvest was also estimated. For example, we found that out of 13 sites with sufficient data on muskrat harvest for analyses, only 6 and 8 of those sites also had long-term monitoring data on waterfowl and SMBs respectively, during overlapping date ranges. Similarly, more fine-scale evaluations, such as comparisons made at the scale of an individual trapping unit or wetland, may reveal patterns in SMB and waterfowl use relative to muskrat abundances that are obscured at the site-level scale, but are outside of the framework of this regional project. Thus, we consider the role of muskrats as an indicator of other wetland wildlife to be inconclusive.

Our comparison of annual muskrat harvest and hut count data collected by the USFWS at the Ottawa NWR represented one of few known attempts to specifically quantify the relationship between harvest and the underlining population status of muskrats. After controlling for extrinsic factors associated with trapper effort, we documented a positive relationship between annual harvest and muskrat abundance. Although we anticipate that this relationship between harvest and hut counts will likely vary across space due to variation in other environmental factors contributing to number of muskrats per hut, this finding is expected to be useful to managers and muskrat management by validating the role of harvest data as an indicator of muskrat abundance at fine spatial scales. In addition, this relationship highlights the value of utilizing muskrat trappers as citizen scientists to monitoring muskrat populations.

Our analyses may be improved through addressing limitations associated with the availability of important datasets during this study. First, the U.S. EPA's NWCA program nationwide effort 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 dataset from this program in our modeling efforts (variables for FQI and VMMI), the data resulting from the 2016-2017 survey was not available prior to the conclusion of our study. Including these additional data would have allowed us to examine the relationship 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. Similarly, the Wetland Extent Tool (WET), developed in collaboration between UCLA and National Aeronautics and Space Administrations (NASA), was also not yet available despite being scheduled for release in early 2021. This tool was expected to provide a more detailed and comprehensive technique for measuring the spatial extent and associated spatial attributes of wetlands throughout the Great Lakes Basin, including 10-m resolution for classifying wetlands at 86% accuracy (Valenti et al. 2020). Once both the 2016-2017 NWCA data and the WET become available, we suggest that this research be repeated in a manner that allows the integration of these important datasets into updated analyses.

MANAGEMENT RECOMMENDATIONS

Based on our interpretation of results, we offer several recommendations for consideration. We acknowledge that our recommendations may not fully integrate site-specific constraints, nor complete considerations of political or social conditions at the local or state level, as these were beyond the scope of our project. However, where possible, we have included broad-level concepts that may be further developed, and we can be part of any more detailed discussions related to our recommendations. Our recommendations, in no particular order, include:

- **Continue to mitigate loss and improve connectivity of wetland ecosystems.** Our results suggest that increased connectivity and area of wetlands were associated with increased county-level muskrat harvest, and putatively, suggested that wetland loss has contributed to widespread declines in muskrat populations. Efforts to promote wetland habitat, including programs such as Great Lakes Conservation Initiative, could therefore serve to increase the abundance of muskrats in the Great Lakes Basin. Given the role of muskrats as ecosystem engineers in wetland communities, wetland management actions that specifically include efforts to increase the abundance and distribution of muskrat populations may synergistically serve to improve wetland function and biodiversity. For planning purposes, connectivity should be considered during creation of new wetlands, if multiple sites are under consideration. If only a single site is available for wetland creation, perhaps future efforts could include adjacent locations to increase connectivity. Regardless, we do not recommend halting the creation of a wetland based solely on lack of connectivity, only that potential alternatives be considered.

- **Investigate the influence of vegetation and drought condition on muskrat populations.** Our analyses revealed potentially important relationships between vegetation condition (as measured by VMMI) and drought (as measured by SPI) at site-level and county-level scales, respectively. Studies evaluating the precise mechanisms driving these relationships could be valuable to understanding and mitigating the factors driving population declines of muskrats throughout their distribution. For example, additional research on the impact of varying levels of vegetation and drought conditions experienced within the Great Lakes Basin on population structure, reproductive status, and body condition of populations of muskrats could inform wetland and muskrat management decisions. Based on data from this project, wetland vegetation condition is expected to occur as a gradient transitioning from relatively high quality in the northwestern Great Lakes Basin (e.g., northeastern MN, northern MI) and decreasing to relatively low quality in the southeastern Great Lakes Basin (e.g., southern MI, OH). Future drought conditions are difficult to predict, but variation is most likely to occur over a large geographic area. Therefore, we recommend that any study evaluating these relationships include multiple study areas widely distributed throughout the Great Lakes Basin. Our team has secured partial funding for such a project and will be implementing this project during 2022.

- **Integrate multiple survey efforts when and where possible to maximize efficiency for data collection and wetland management.** 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 was constrained by too few data that were spatially and temporally consistent within our study area. We recommend identification of wetland areas of interest, particularly those areas where consistent monitoring efforts to survey populations of other wetland wildlife (i.e., SMB, waterfowl, amphibians) are or can be established, and where long-term wetland monitoring programs (i.e., NWCA, ORAM, or MWCA) are ongoing, for standardized and relatively comprehensive surveys for muskrats. This would include hut-count surveys, basic surveys of wetland vegetation and water quality, weather, and other data. If harvest occurs on these sites, then collection of harvest data can also be standardized according to our next recommendation.

- **Standardize collection of harvest data for all furbearing species to increase the utility of these data.** Based on current annual statewide furharvester surveys, we utilized county-level data from Minnesota, Michigan, and Ohio to account for trapper effort either by quantifying trap-days or days spent trapping when inferring population-level effects on muskrats. Our ability to quantify trapper effort during our site-level analyses varied by site. Existing site-level harvest data spanned from no data associated with harvest effort to daily trapping logs whereby trap-hours per day per individual trapping unit were recorded. Standardization of these harvest data, including for harvest effort, at the county and site levels would allow for a much more robust evaluation of muskrat harvest and populations trends, and consequently, improved management of both muskrats and wetlands. We also recommend a mandatory process to help ensure a sufficient response rate. For states or sites where such a process is not mandatory, we recommend consideration of developing and implementing the process in close coordination with the respective state trapping association (and possibly other such groups) in each jurisdiction. This stakeholder coordination would allow for the transfer of information in two directions, and a successful process would increase the quantity and quality of information available to evaluate population-level effects of muskrat populations. Also, this extends beyond muskrats, as this would also be of benefit for other harvested furbearing species in each state. Although several state wildlife agencies have implemented mandatory harvest reporting related to trapping (see Association of Fish and Wildlife Agencies 2016:137–139), we acknowledge that transitioning from voluntarily to mandatory may be a lengthy and relatively challenging process, but the transition would be very beneficial for management and the transition need not be abrupt (e.g., no penalties for the first 1–2 years of implementation as an adjustment period). We also acknowledge that certain constraints may not allow for implementation of mandatory surveys, and that enforcement of survey submissions may not be tractable. In these instances, and when voluntary surveys may be utilized, we recommend focusing on increasing the participation rates to improve data quantity. We have partnered with many trapping organizations for various purposes and could develop this recommendation further, if requested.

- **Replicate our analysis once delayed data and toolsets become available.** Our results are valid based on our data, but our results are also limited to the data (and tools) that were available during our project. Data derived from the U.S. EPA's 2016 NWCA program and NASA's Wetland Extent Tool could contribute valuable information on the relationship between wetland condition and spatial extent on muskrat harvest and underlying population dynamics. Unfortunately, neither of these resources were available before the conclusion of our project, but the opportunity exists to integrate these data and tools, which are expected to become available by 2022. By replicating our analysis with these additional data and cutting-edge tools, we could provide additional insight into population declines, management opportunities, and potential role as indicator species, for muskrat population within the Great Lakes Basin. Although this may not change our current recommendations, it could refine them, as well as develop new recommendations that are as pragmatic.

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Table 1. Selected information collected through annual furharvester surveys by Michigan Department of Natural Resources, Minnesota Department of Natural Resources, and Ohio Department of Natural Resources. Date ranges of data used in this project are specified for each state.

State Information collected	Date range
Michigan	
Counties were muskrat harvest occurred	2000–2018
Number of muskrats harvested in each county	2000–2018
Number of days spent trapping for muskrats in each county	2000–2018
Minnesota	
County were muskrat harvest occurred	2002–2018
Number of muskrats harvested in county	2002–2018
Number of traps set for muskrats in county	2006–2018
Number of days spent trapping for muskrats in each county	2006–2018
Ohio	
Counties were majority of harvest occurred	2008–2018
Number of muskrats harvested	2008–2018
Number of days spent trapping muskrats	2008–2018
Average number of traps set per day spent trapping muskrats	2008–2018

Table 2. Details on all site-level datasets documenting annual muskrat harvest included in model sets of our analyses of per capita muskrat harvest (PCHM; n = 13), secretive marsh bird (SMB) richness (n = 8), or waterfowl richness (n = 6) from national wildlife refuges or state-managed areas distributed through the Great Lakes Basin, USA, during 2000–2018. Sites and number of years of data included in model sets for up to 3 separate analyses are indicated in the Model Set column depending on the availability of data for a given site. Site ID corresponds to Fig. 2. Data source indicates the state or federal wildlife management agencies that provided the specified dataset on muskrat harvest for this project and are abbreviated as: MIDNR = Michigan Department of Natural Resources, MNDNR = Minnesota Department of Natural Resources, ODNR = Ohio Department of Natural Resources, USFWS = U.S. Fish and Wildlife Services. Site names abbreviations include the following: NWR = National Wildlife Refuge, SGA = State Game Area, and SWA = State Wildlife Area.

Site ID	Site	State	Harvest Data Source	Harvest Data Date Range	Model Set (number of yr of available data)		
					PCHM	SMB	Waterfowl
1	Carlos Avery State WMA	MN	MNDNR	2000–2018	17	0	0
2	Cedar Point NWR	OH	USFWS	2001–2018	16	0	0
3	Crow Island SGA	MI	MIDNR	2009–2018	8	4	7
4	Harsens Island SWA	MI	MIDNR	2005–2016	11	8	11
5	Horicon NWR	WI	USFWS	2000–2018	17	7	5
6	Minnesota Valley NWR	MN	USFWS	2000–2014	14	7	0
7	Nayanquing Point SWA	MI	MIDNR	2009–2018	8	0	8
8	Necedah NWR	WI	USFWS	2000–2018	17	0	0
9	Ottawa NWR	OH	USFWS	2000–2018	17	7	0
10	Point Mouillee SGA	MI	MIDNR	2000–2014	14	2	8
11	Sherburne NWR	MN	USFWS	2000–2006	6	3	0
12	Shiawassee NWR	MI	USFWS	2000–2018	17	0	5
13	Wigwam Bay SWA	MI	MIDNR	2009–2018	8	2	0

Table 3. Details on all site-level datasets documenting annual muskrat harvest compiled but excluded from our analyses (*n* = 13) from 1 national wildlife refuges and 12 state-managed areas distributed through the Great Lakes Basin, USA. Datasets were excluded from analyses due to spatial or temporal limitations of the data. For each dataset, we provide a description of the rationale for excluding the data from our analyses. Management agencies are abbreviated as follows: ILDNR = Illinois Department of Natural Resources, INDNR = Indiana Department of Natural Resources, MIDNR = Michigan Department of Natural Resources, MNDNR = Minnesota Department of Natural Resources, USFWS = U.S. Fish and Wildlife Services. Site names abbreviations include the following: FWA = Fish and Wildlife Area, NWR = National Wildlife Refuge, SGA = State Game Area, and WMA = Wildlife Management Area.

Site	State	Data source	Reason to exclude
Blue Grass FWA	IN	INDNR	Number of muskrat trappers not provided
Goose Pond FWA	IN	INDNR	Unable to reliably determine number of trappers targeting muskrats
Interlake FWA	IN	INDNR	Less than 5 years of muskrat harvest available during study
Kingsbury FWA	IN	INDNR	Annual number of muskrat trappers not provided
Lac qui Parle WMA	MN	MNDNR	Date range of muskrat harvest data provided did not overlap with study
Lasalle FWA	IN	INDNR	Annual number of muskrat trappers not provided
Nicollette WMA	MN	MNDNR	Annual number of muskrat trappers not provided
Roseau River State WMA	MN	MNDNR	Unable to reliably determine number of trappers targeting muskrats
Seney NWR	MI	USFWS	Date range of muskrat harvest data provided did not overlap with study
Shiawassee River SGA	MI	MIDNR	Annual number of muskrat trappers not provided
Sugar Ridge FWA	IN	INDNR	Annual number of muskrat trappers not provided
Tamarac NWR	MN	USFWS	Unable to reliably determine number of trappers targeting muskrats
Tri-County FWA	IN	INDNR	Annual number of muskrat trappers not provided for >5 years

Table 4. Names, descriptions, and data sources for all independent variables used to develop model sets for both the county and site-level analyses from data collected throughout the Great Lakes Basin, USA, during 2000–2018. Data sources are abbreviated as follows: Avian Surveys = annual secretive marsh bird (SMB) and waterfowl surveys conducted by various agencies (see methods), Furbuyer Surveys = annual fur buyer surveys (see methods), gridMET = gridded dataset of surface meteorological variables (Abatzogluou 2013); NLCD = National Land Cover Database, NWI = National Wetland Inventory (U.S. Fish and Wildlife Service. 2021), PRISM = PRISM Climate Group (PRISM Climate Group, 2021), US EPA = U.S. EPA's Ecoregion Classification (Omernik and Griffith. 2014), Wetland = a combination of data derived from the U.S. EPA's National Wetland Condition Assessment program (U.S. EPA 2016), Ohio Environmental Protection Agency's Ohio Rapid Assessment Monitoring (Gara and Schumacher 2015), and Minnesota Pollution Control Agency's Minnesota Wetland Condition Assessment (Bourdaghs et al. 2019), US BLS = U.S. Bureau of Labor Statistics (U.S. BLS 2021), and US EIA = U.S. Energy Information Administration (U.S. EIA 2021).

Variable group Variable	Description	Data source
Weather		
Summer Temp	Annual deviation from prior 10-year average in summer temperature	PRISM
Winter Temp	Annual deviation from prior 10-year average in winter temperature	PRISM
Summer Precip	Annual deviation from prior 10-year average in summer precipitation	PRISM
Winter Precip	Annual deviation from prior 10-year average in winter precipitation	PRISM
$PDSI_t$[a]	Palmer Drought Severity Index for year harvest season was initiated	gridMET
$PDSI_{t-1}$[a]	Palmer Drought Severity Index for year preceding harvest season	gridMET
SPI_t	Standardize Precipitation Index for year harvest season was initiated	gridMET
SPI_{t-1}	Standardize Precipitation Index for year preceding harvest season	gridMET
Landscape-scale habitat attribute[b]		
Area Agriculture	Area (%) reclassified as combined agriculture category	NLCD
Area Developed	Area (%) reclassified as combined developed category	NLCD
Area Wetlands	Area (%) reclassified as combined wetland category	NLCD
Area Woody Wetlands	Area (%) classified as woody wetlands	NLCD
Area Emergent Wetlands	Area (%) classified as emergent herbaceous wetlands	NLCD
Patch Area	Average size (km^2) of patches from combined wetland category	NLCD
Connectivity	Average distance (m) between wetland patches	NLCD
Largest Patch	Largest area (km^2) of a single wetland patch	NLCD
Number of Patches	Total number of wetlands patches	NLCD

Table 4. (Cont'd)

Variable group Variable	Description	Data source
Landscape-scale habitat attributes[b] (cont'd)		
Area Emergent Wetlands NWI[a]	Area (%) classified as freshwater emergent wetlands	NWI
Area Shrub Wetlands NWI[a]	Area (%) classified as forested shrub wetlands	NWI
Area Riverine[a]	Area (%) classified as riverine	NWI
Area Wetlands NWI[a]	Area (%) reclassified as combined wetland category (NWI)	NWI
Ecoregion[c]	Majority Level I ecoregion	US EPA
Wetland Vegetation Condition[b]		
FQI[a]	Average Interpolated Floristic Quality Index	Wetland
VMMI	Average Interpolated Vegetative Multimetric Index	Wetland
Trapper Effort[d]		
Pelt Price	Price (US$) of raw muskrat pelt sold in state	Furbuyer Surveys
Gas Price	Average gasoline price (US$) for all grades sold in state	US EIA
Unemployment	Average unemployment rate for state	US BLS
Sample Effect for SMBs and Waterfowl Richness[e]		
Sample Area	Area (km^2) of the site	Avian Surveys
Number of Samples	Number of surveys conducted within a site	Avian Surveys
Number of Individuals	Number of individuals detected during all surveys	Avian Surveys

[a]As a result of high correlation ($|r| > 0.7$) with a similar variable, variable was not included in model sets.
[b]Variables were calculated over the spatial extent of each county for all county-level analyses or the spatial extent of all area contained within 10 km of the property boundaries of each site for all site-level analyses.
[c]Variable not included in site-level analyses because 12 of 13 sites were contained within a single ecoregion.
[d]Variables included in all models used in model sets where trapper effort was not directly quantified in the dependent variable.
[e]Variables included in all models used in model sets to evaluate secretive marsh bird (SMB) and waterfowl richness.

Table 5. List of all datasets compiled but excluded from analyses due to spatial or temporal limitations of the data collected from a variety of sources and occurring throughout Michigan, Minnesota, and Ohio during 2000-2018. For each dataset, we provide a description of the spatial and temporal extent and rationale for excluding the data from our analyses. Data sources are abbreviated as follows: CWMP = Coastal Wetland Monitoring Program (Uzarski et al. 2016), MMP = Marsh Monitoring Program's datasets (Birds Canada 2021), MWADC = Midwest Avian Data Center regional marsh bird survey (Koch et al. 2010), ODNR-1 = Ohio Department of Natural Resources study of muskrat contaminates (ODNR 2016), ODNR-2 = Ohio Department of Natural Resources annual waterfowl survey data (ODNR, unpublished data).

Dataset type	Description	Reason to exclude	Data source
Muskrat Toxins	Muskrats (n = 40) sampled from 24 counties collected over 1 year	Too few samples, limited temporal coverage, limited spatial coverage	ODNR-1
Waterfowl	Surveys of managed areas (n = 14) from 9 counties in Ohio collected over regularly 10 years	Limited spatial coverage, unable to extrapolate to county	ODNR-2
Marsh Birds	Surveys of 50-m points (n = 270) from 254 counties collected intermittently over 9 years	Unable to extrapolate to county, limited temporal coverage	MWADC
Marsh Birds	Surveys of 50-m points (n = 765) from 54 counties collected intermittently over 10 years	Limited spatial coverage, limited temporal coverage, unable to extrapolate to county	MMP
Amphibians	Surveys of 50-m points (n = 1,409) from 66 counties collected intermittently over 10 years	Limited spatial coverage, limited temporal coverage, unable to extrapolate to county	MMP
Wetland Condition	Surveys of wetlands (n = 329) from 42 counties collected intermittently over 5 years	Limited temporal coverage, limited spatial coverage	CWMP

Table 6. Summary statistics of county-level annual muskrat harvest data reported to furharvester surveys conducted by state wildlife agencies in Michigan, Minnesota, and Ohio, USA, from 2000–2018. Data were obtained via voluntary surveys provided to a portion of license muskrat trappers in each state. Trappers were asked to report the county or counties where the majority of their muskrat trapping occurred. All values related to muskrat harvest represent reported totals only and do not account for unreported harvest.

Description	Michigan	Minnesota	Ohio
Number of counties	83	87	88
Date range of data	2000–2018	2002–2018	2008–2018
Dates of harvest season	1 Nov–1 Mar[a]	23 Oct–15 May	10 Nov–28 Feb[b]
Number of harvest seasons	18	16	10
Total number of muskrats harvested	303,195	1,262,004	284,329
Average annual number of muskrats harvested per county	213.5	922.5	365.9
Standard deviation in annual number of muskrats harvested per county	282.9	1,548.0	495.0
Total number of trappers	9,007	27,004	7,501
Average annual number of trappers per county	6.3	19.7	9.6
Standard deviation annual number of trappers per county	4.5	21.5	8.7

[a]Start date varies ±10 days for each of three trapping zones.

[b]End date extended to 15 March for Erie, Ottawa, Sandusky, and Lucas counties.

Table 7. Selection results of 86 models for a county-level analysis of muskrat harvest data collected for all counties (n = 258) in Michigan during 2000–2018, Minnesota during 2002–2018, and Ohio during 2008–2018, USA. The dependent variable used in this model set was per capita muskrat harvest (PCMH). 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 best model within the model set, and w = AIC_c weight. County and harvest season were included as random effects for all models. Pairwise interaction terms are denoted by the * symbol. Top 10 models based on AIC_c are shown. Variable descriptions are detailed in Table 4.

Rank	Model	K	LL	ΔAIC_c	w
1	Connectivity * Ecoregion + SPI_t * Ecoregion + $SPI_{t\text{-}1}$ * Ecoregion	18	−4449.00	0.00	0.60
2	Winter Temp * Ecoregion + SPI_t * Ecoregion + $SPI_{t\text{-}1}$ * Ecoregion	18	−4450.03	2.07	0.22
3	Area Wetland * Ecoregion + SPI_t * Ecoregion + $SPI_{t\text{-}1}$ * Ecoregion	18	−4450.49	2.98	0.14
4	Area Woody Wetlands * Ecoregion + SPI_t * Ecoregion + $SPI_{t\text{-}1}$ * Ecoregion	18	−4451.62	5.23	0.04
5	SPI_t * Ecoregion + $SPI_{t\text{-}1}$ * Ecoregion	15	−4460.97	17.89	<0.01
6	Winter Temp * Ecoregion + SPI_t * Ecoregion	15	−4473.03	42.00	<0.01
7	Summer Temp * Ecoregion + SPI_t * Ecoregion	15	−4474.45	44.85	<0.01
8	Connectivity + SPI_t + $SPI_{t\text{-}1}$ * Ecoregion	12	−4491.34	72.58	<0.01
9	SPI_t + $SPI_{t\text{-}1}$ + Ecoregion	11	−4493.08	74.04	<0.01
10	Summer Temp * Ecoregion + Winter Temp * Ecoregion	15	−4493.10	82.15	<0.01

Table 8. Selection results of 53 models for a county-level statewide analysis of muskrat harvest data collected during 2006–2018 for all counties (n = 87) in Minnesota, USA. The dependent variable used in this model set was muskrat catch per trap-day (CPTD). 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 best model within the model set, and w = AIC_c weight. County and harvest season were included as random effects for all models. Pairwise interaction terms are denoted by the * symbol. Top 10 models based on AIC_c are shown. Variable descriptions are detailed in Table 4.

Rank	Model	K	LL	ΔAIC_c	w
1	SPI_t + SPI_{t-1}	6	−1265.27	0.00	0.41
2	SPI_t + SPI_{t-1} + Connectivity	7	−1264.92	1.33	0.21
3	SPI_t + SPI_{t-1} + Winter Temp	7	−1265.24	1.96	0.15
4	SPI_t + SPI_{t-1} + Summer Temp	7	−1265.27	2.02	0.15
5	SPI_t	5	−1268.84	5.11	0.03
6	SPI_t + Winter Temp	6	−1268.76	6.99	0.01
7	SPI_t + Summer Temp	6	−1268.81	7.08	0.01
8	SPI_t * Ecoregion + SPI_{t-1} * Ecoregion	12	−1263.28	8.24	<0.01
9	SPI_t * Ecoregion + SPI_{t-1} * Ecoregion + Connectivity * Ecoregion	15	−1260.26	8.38	<0.01
10	SPI_t * Ecoregion + SPI_{t-1} * Ecoregion + Area Wetlands * Ecoregion	15	−1261.16	10.17	<0.01

Table 9. Selection results of 51 models for a county-level statewide analysis of muskrat harvest data collected during 2008–2018 for all counties (n = 88) in Ohio, USA. The dependent variable used in this model set was muskrat catch per trap-day (CPTD). 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 best model within the model set, and w = AIC_c weight. County and harvest season were included as random effects for all models. Pairwise interaction terms are denoted by the * symbol. Top 10 models based on AIC_c are shown. Variable descriptions are detailed in Table 4.

Rank	Model	K	LL	ΔAIC_c	w
1	Area Emergent Wetlands + Connectivity	6	−851.13	0.00	0.34
2	Area Emergent Wetlands + VMMI	6	−851.47	0.69	0.24
3	Area Emergent Wetlands	5	−852.78	1.26	0.18
4	Area Emergent Wetlands + SPI_t	6	−852.77	3.28	0.07
5	Area Wetlands	5	−853.95	3.61	0.06
6	Area Emergent Wetlands + SPI_t + $SPI_{t\text{-}1}$	7	−852.72	5.22	0.02
7	Connectivity	5	−854.98	5.68	0.02
8	Connectivity + Patch Area	6	−854.03	5.80	0.02
9	Area Wetlands + SPI_t + $SPI_{t\text{-}1}$	7	−853.89	7.56	<0.01
10	Area Woody Wetlands + Connectivity	6	−854.92	7.59	<0.01

Table 10. Selection results of 65 models for a county-level statewide analysis of muskrat harvest data collected during 2007–2018 for all counties (n = 83) in Michigan, USA. The dependent variable used in this model set was muskrat catch per days spent trapping (CPD). 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 best model within the model set, and w = AIC_c weight. County and harvest season were included as random effects for all models. Since number of traps set per day (i.e., trap-days) was not quantified during the Michigan furharvester survey, all models within this model set included independent variables of pelt price, unemployment, and gas price to account for trapper effort. Pairwise interaction terms are denoted by the * symbol. Top 10 models based on AIC_c are shown. Variable descriptions are detailed in Table 4.

Rank	Model	K	LL	ΔAIC_c	w
1	Largest Wetland + Area Wetlands * Ecoregion	11	−1200.75	0.00	0.55
2	Largest Wetland * Ecoregion + Area Wetlands * Ecoregion	12	−1200.40	1.53	0.28
3	Largest Wetland * Ecoregion + SPI_t	11	−1203.55	5.59	0.03
4	Largest Wetland + Area Wetlands * Ecoregion	10	−1204.64	5.73	0.03
5	Area Wetlands * Ecoregion	10	−1204.69	5.83	0.03
6	Area Woody Wetlands * Ecoregion	10	−1205.12	6.76	0.02
7	Area Wetlands * Ecoregion + Patch Area * Ecoregion	12	−1203.53	7.62	0.01
8	Patch Area * Ecoregion	10	−1205.69	7.82	0.01
9	Patch Area + Area Wetlands * Ecoregion	11	−1204.67	7.83	0.01
10	Largest Wetland * Ecoregion	10	−1205.77	8.00	<0.01

Table 11. Selection results of 57 models for a site-level analysis of muskrat harvest data collected for 7 national wildlife refuges and 6 state-managed areas occurring within the Great Lakes Basin and associated states, USA. The dependent variable used in this model set was per capita muskrat harvest (PCMH). Date ranges of harvest data varied by site (Table 4). 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 best model within the model set, and w = AIC_c weight. Site and harvest season were included as random effects for all models. Top 10 models based on AIC_c are shown. Variable descriptions are detailed in Table 4.

Rank	Model	K	LL	ΔAIC_c	w
1	VMMI	8	−233.93	0.00	0.28
2	VMMI + Area	9	−234.19	2.72	0.07
3	VMMI + Area Emergent Wetlands	9	−234.26	2.85	0.07
4	VMMI + Largest Patch	9	−234.33	3.00	0.06
5	VMMI + Area Woody Wetlands	9	−234.36	3.05	0.06
6	VMMI + Area Wetlands	9	−234.55	3.43	0.05
7	VMMI + SPI_t	9	−234.72	3.77	0.04
8	Number of Wetlands	8	−235.94	4.00	0.04
9	NULL	7	−237.21	4.36	0.03
10	Patch Area	8	−-236.30	4.72	0.03

Table 12. Selection results of 105 models for a site-level analysis of the relationship between secretive marsh bird (SMB) richness and per capita muskrat harvest (PCMH) data collected for 3 national wildlife refuges and 5 state-managed areas occurring within the Great Lakes Basin, USA. The dependent variable used in this model set was SMB richness, measured at the number of unique SMB species detected during all surveys. Variables for sample area, number of samples, and number of individuals detected were included in all models to control for the influence of sampling effects when calculating richness (Dunn et al. 2009, Gotelli and Colwell 2011). 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 best model within the model set, and w = AIC_c weight. Site and harvest season were included as random effects for all models. Top 10 models based on AIC_c are shown. Variable descriptions are detailed in Table 4.

Rank	Model	K	LL	ΔAIC_c	w
1	NULL	6	−77.78	0.00	0.09
2	SPI_t	7	−76.76	0.85	0.06
3	Number of Patches	7	−76.79	0.91	0.05
4	VMMI	7	−77.10	1.52	0.04
5	Patch Area	7	−77.22	1.78	0.04
6	Area Developed	7	−77.25	1.83	0.03
7	Area Woody Wetland	7	−77.50	2.33	0.03
8	Summer Temp	7	−77.57	2.47	0.03
9	Area Wetland	7	−77.60	2.52	0.02
10	PCMH	7	−77.67	2.66	0.02

Table 13. Selection results of 102 models for a site-level analysis of the relationship between waterfowl richness and per capita muskrat harvest (PCMH) data collected for 2 national wildlife refuges and 4 state-managed areas occurring within the Great Lakes Basin, USA (Table 4, Fig. 2). The dependent variable used in this model set was waterfowl richness, measured at the number of unique waterfowl species detected during all surveys. Variables for sample area, number of samples, and number of individuals detected were included in all models to control for the influence of sampling effects when calculating richness (Dunn et al. 2009, Gotelli and Colwell 2011). 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 best model within the model set, and w = AIC_c weight. Site and harvest season were included as random effects for all models. Top 10 models based on AIC_c are shown. Variable descriptions are detailed in Table 4.

Rank	Model	K	LL	ΔAIC_c	w
1	Number of Patches	7	−128.66	0.00	0.14
2	Summer Precip	7	−129.41	1.50	0.05
3	NULL	6	−130.96	1.75	0.05
4	Patch Area	7	−129.58	1.83	0.05
5	Connectivity + Area Woody Wetland	8	−128.13	1.94	0.04
6	Patch Area + Summer Precip	8	−128.17	2.03	0.04
7	Area Wetlands	7	−129.82	2.31	0.04
8	Area Agriculture	7	−130.00	2.68	0.03
9	Winter Precip	7	−130.07	2.81	0.03
10	Number of Patches + PCMH	8	−128.59	2.86	0.03

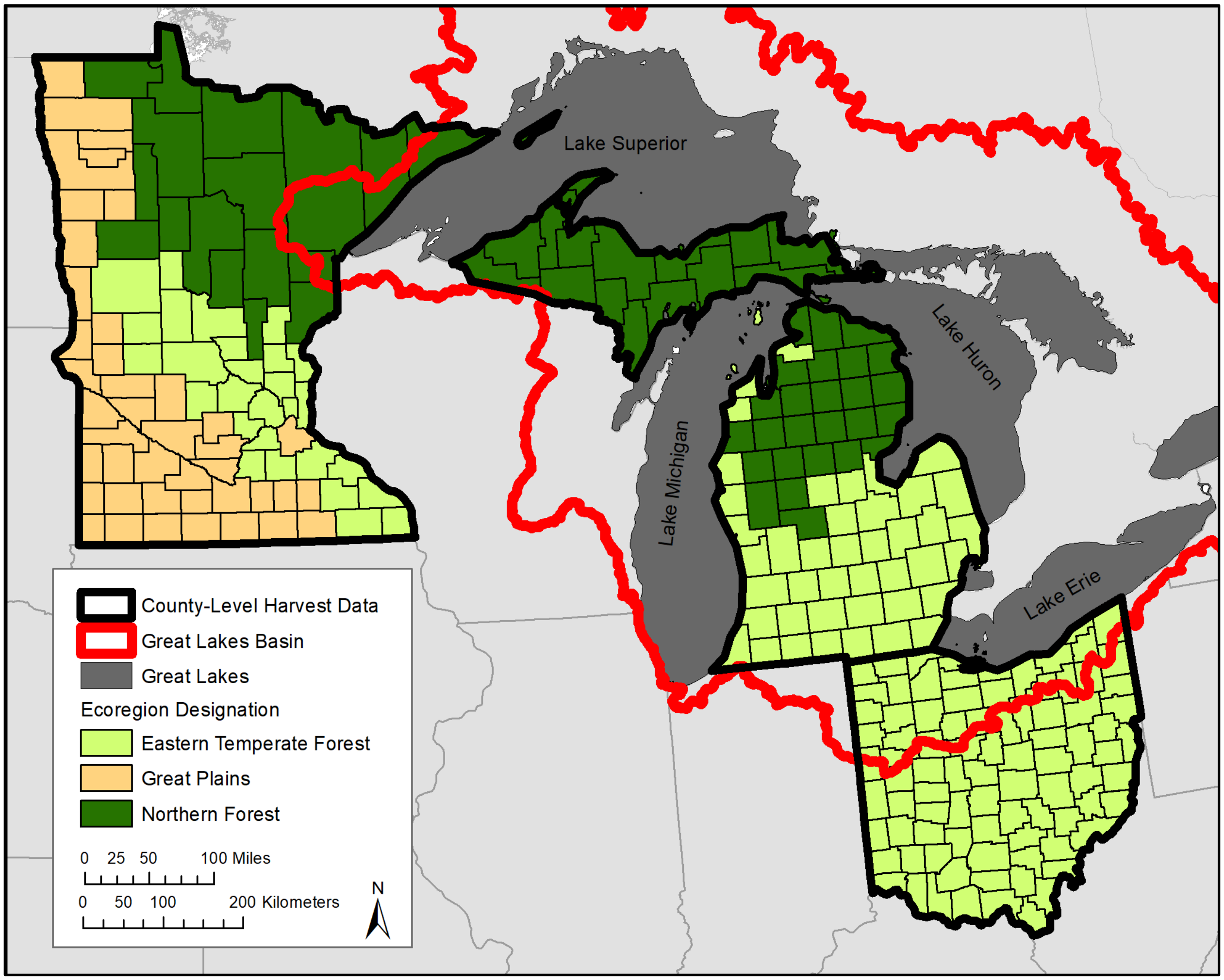
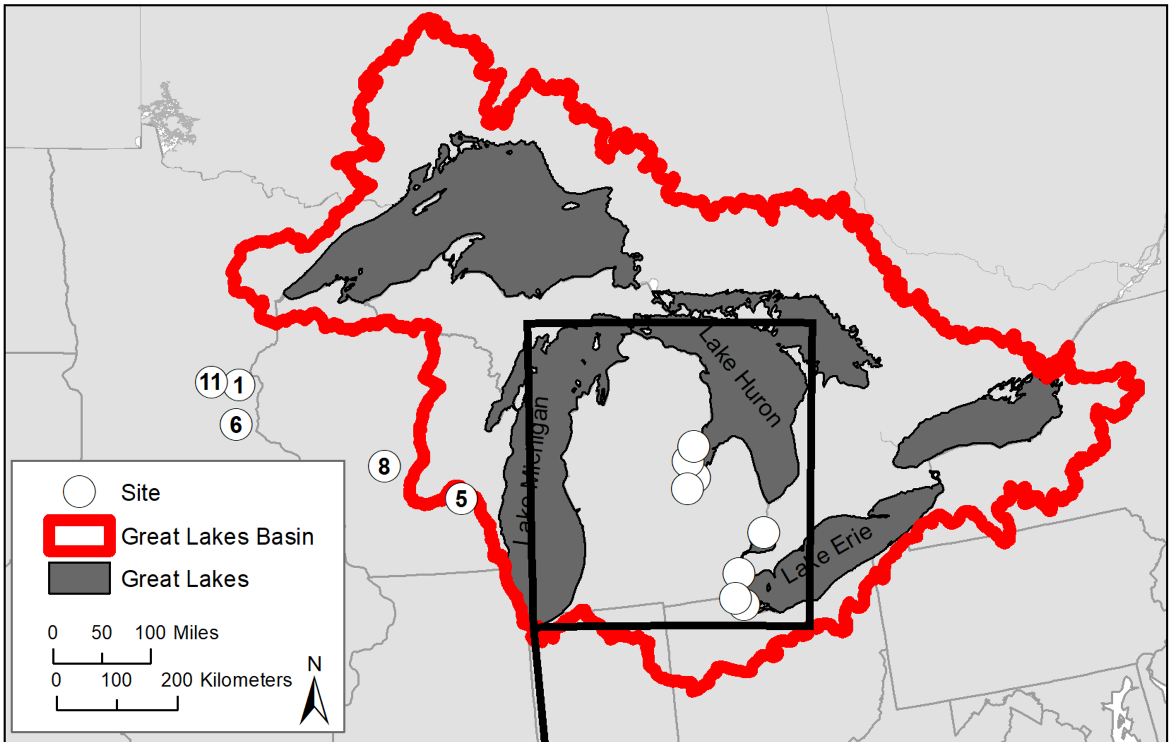
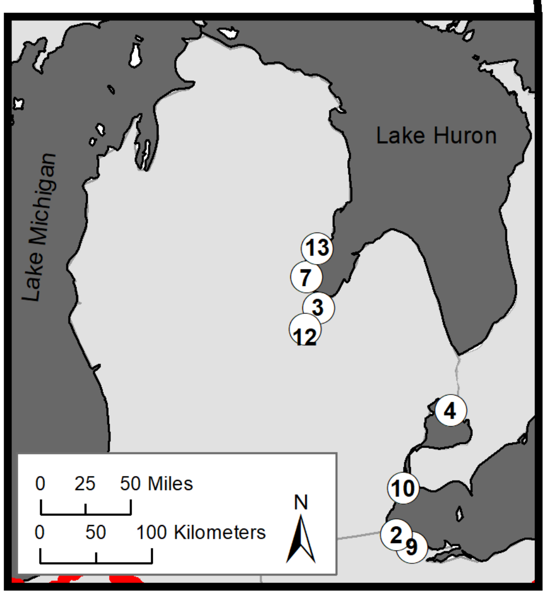


Fig. 1. Spatial distribution and ecoregion designation of counties (n = 258) representing the spatial units used to evaluate county-level per capita muskrat harvest (PCHM) both regionally and for each of the states of Michigan, Minnesota, and Ohio, USA. Ecoregion designation was derived from Level I ecoregions produced by the EPA and assigned to each county by majority area.





Site ID	Site
1	Carlos Avery State WMA, MN
2	Cedar Point NWR, OH
3	Crow Island SGA, MI
4	Harsens Island SWA, MI
5	Horicon NWR, WI
6	Minnesota Valley NWR, MN
7	Nayanquing Point SWA, MI
8	Necedah NWR, WI
9	Ottawa NWR, OH
10	Point Mouillee SGA, MI
11	Sherburne NWR, MN
12	Shiawassee NWR, MI
13	Wigwam Bay SWA, MI

Fig. 2. Spatial distribution of 7 national wildlife refuges and 6 state-managed areas with sufficient data on annual muskrat harvest to include in our model sets evaluating per capita muskrat harvest (PCMH) within 4 states in the Great Lakes Basin, USA. Muskrat harvest data for each site was included in up to 3 separate analyses depending on the availability of corresponding data sets for secretive marsh birds and waterfowl populations. Model set inclusion and date ranges of harvest data varied by site (Table 2). Site names abbreviations include the following: NWR = National Wildlife Area, SGA = State Game Area, SWA = State Wildlife Area, and WMA = Wildlife Management Area.

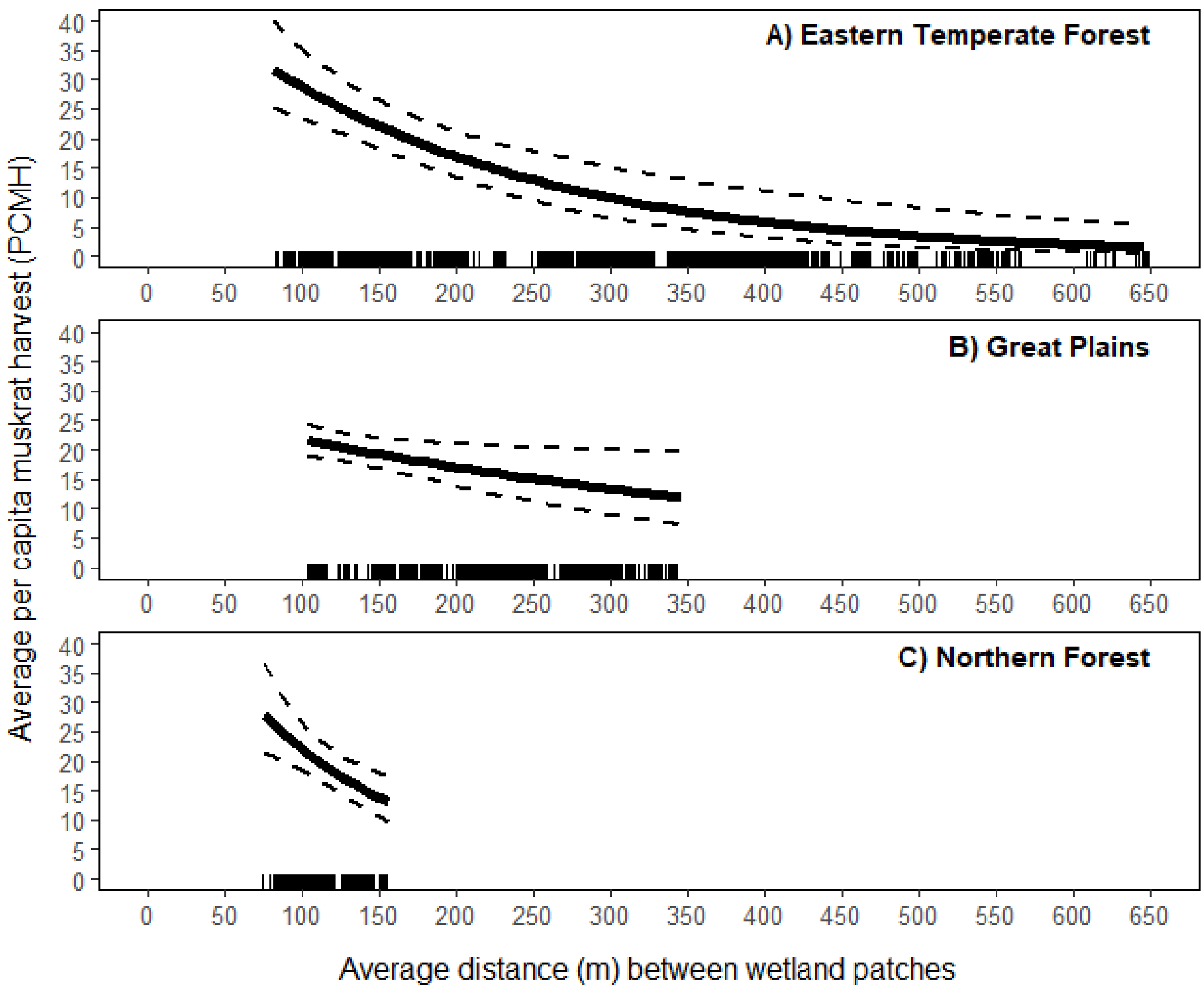


Fig. 3. Relationship between annual reported per capita muskrat harvested (PCMH) per county and average distance (m) between wetland patches (Connectivity) per county by ecoregions A) Eastern Temperate Forest, B) Great Plains, and C) Northern Forest based on furharvester survey data collected from 3 states within the Great Lakes Basin, including Michigan during 2007–2018, Minnesota during 2000–2018, and Ohio during 2008–2018, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 55 models (Table 7, model 1) where all other model variables were held at their average value. Data included 3,715 county-harvest season combinations. Distribution of actual values for Connectivity are shown as a rug plot along the *x*-axis for each panel, respectively.

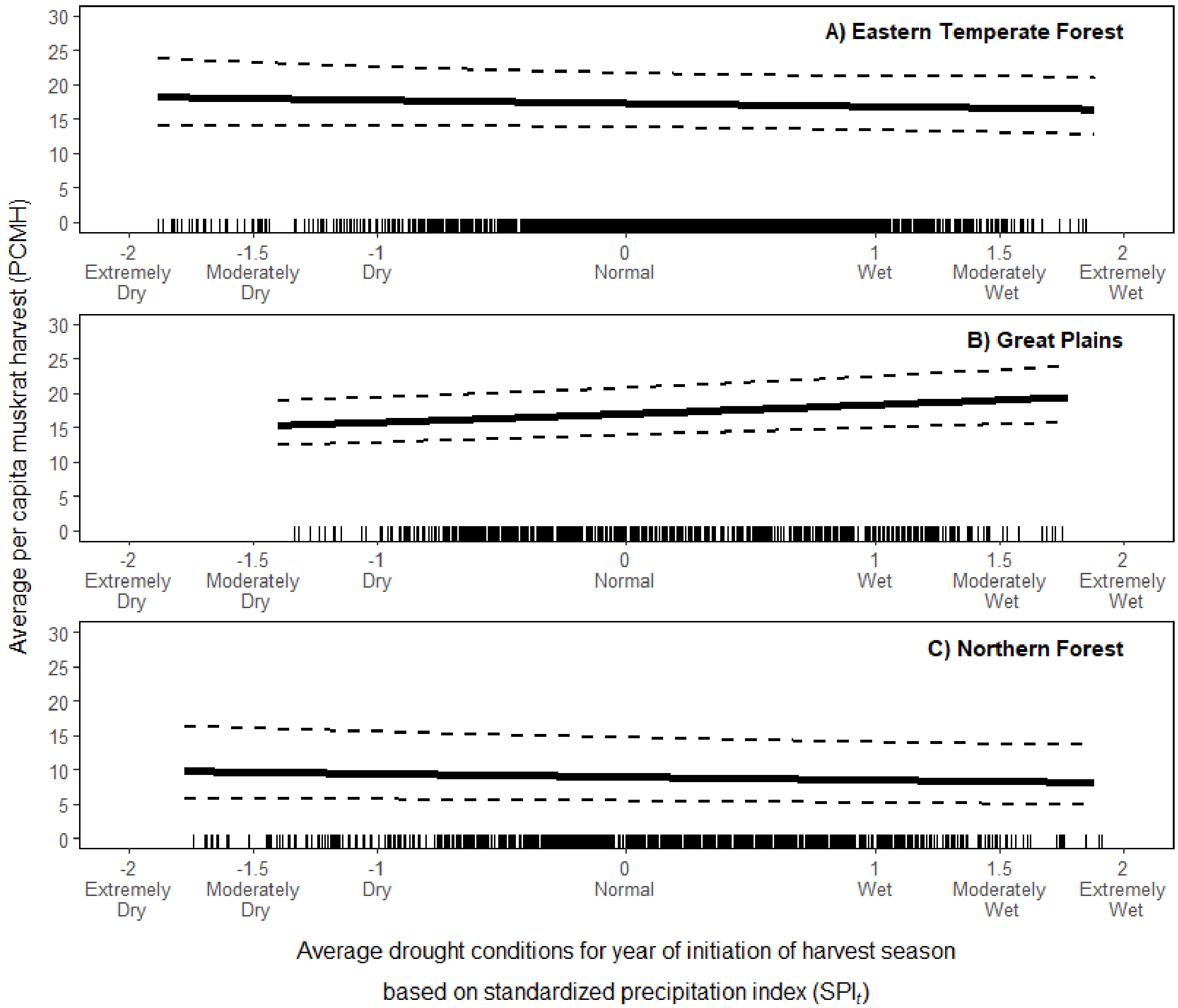


Fig. 4. Relationship between annual reported per capita muskrat harvested (PCMH) per county and drought conditions for year in which harvest season was initiated as measured by annual standardized precipitation index (SPI_t) by ecoregions A) Eastern Temperate Forest, B) Great Plains, and C) Northern Forest. Data on PCMH were derived from furharvester survey data collected from 3 states within the Great Lakes Basin, including Michigan during 2007–2018, Minnesota during 2000–2018, and Ohio during 2008–2018, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 60 models (Table 7, model 1) where all other model variables were held at their average value. Data included 3,715 county-harvest season combinations. Distribution of actual values for SPI_t are shown as a rug plot along the *x*-axis for each panel, respectively.

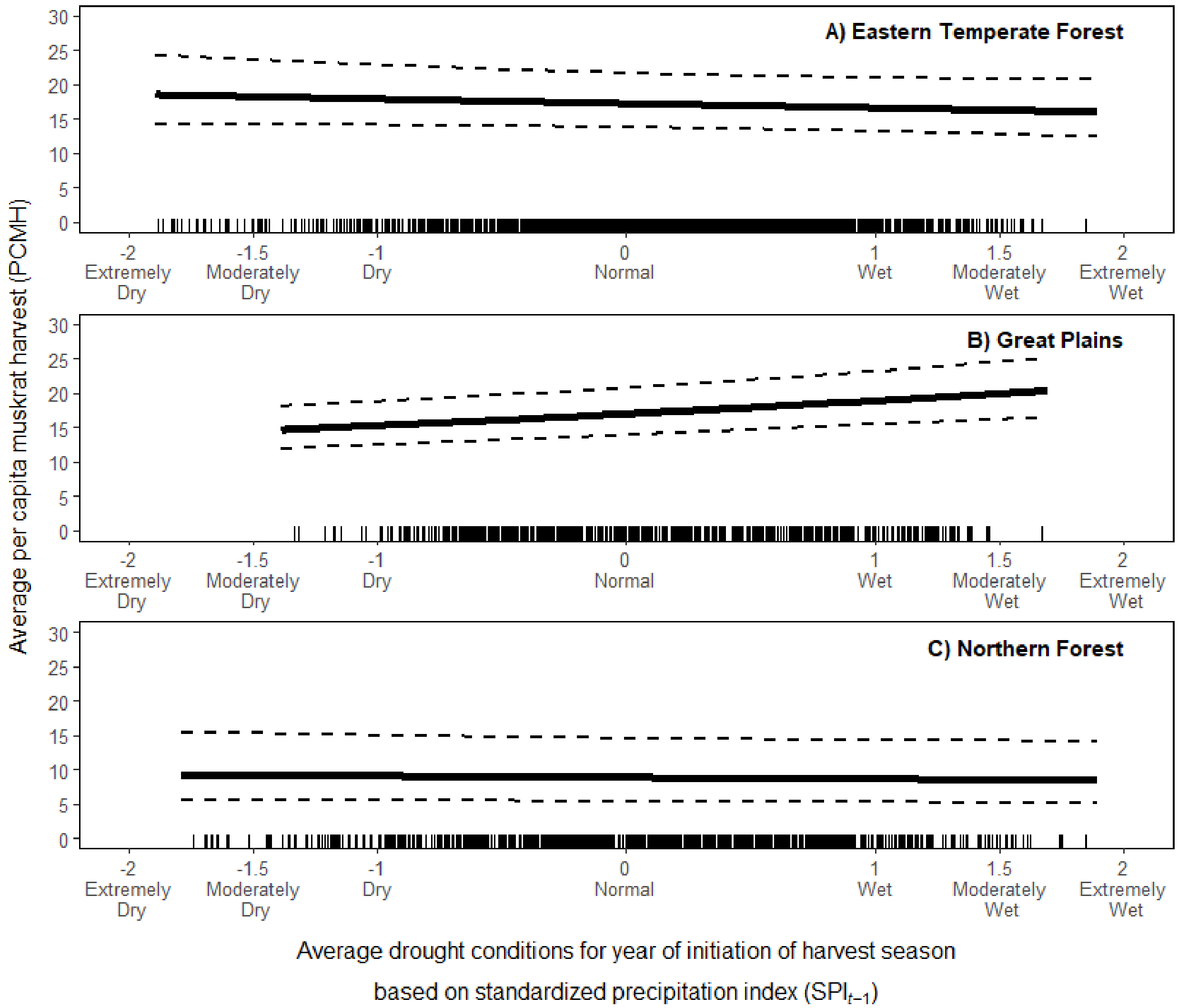


Fig. 5. Relationship between annual reported per capita muskrat harvested (PCMH) per county and drought conditions for year preceding the year in which harvest season was initiated as measured by annual standardized precipitation index ($SPI_{t\text{-}1}$) by ecoregions A) Eastern Temperate Forest, B) Great Plains, and C) Northern Forest. Data on PCMH were derived from furharvester survey data collected from 3 states within the Great Lakes Basin, including Michigan during 2007–2018, Minnesota during 2000–2018, and Ohio during 2008–2018, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 60 models (Table 7, model 1) where all other model variables were held at their average value. Data included 3,715 county-harvest season combinations. Distribution of actual values for $SPI_{t\text{-}1}$ are shown as a rug plot along the x-axis for each panel, respectively.

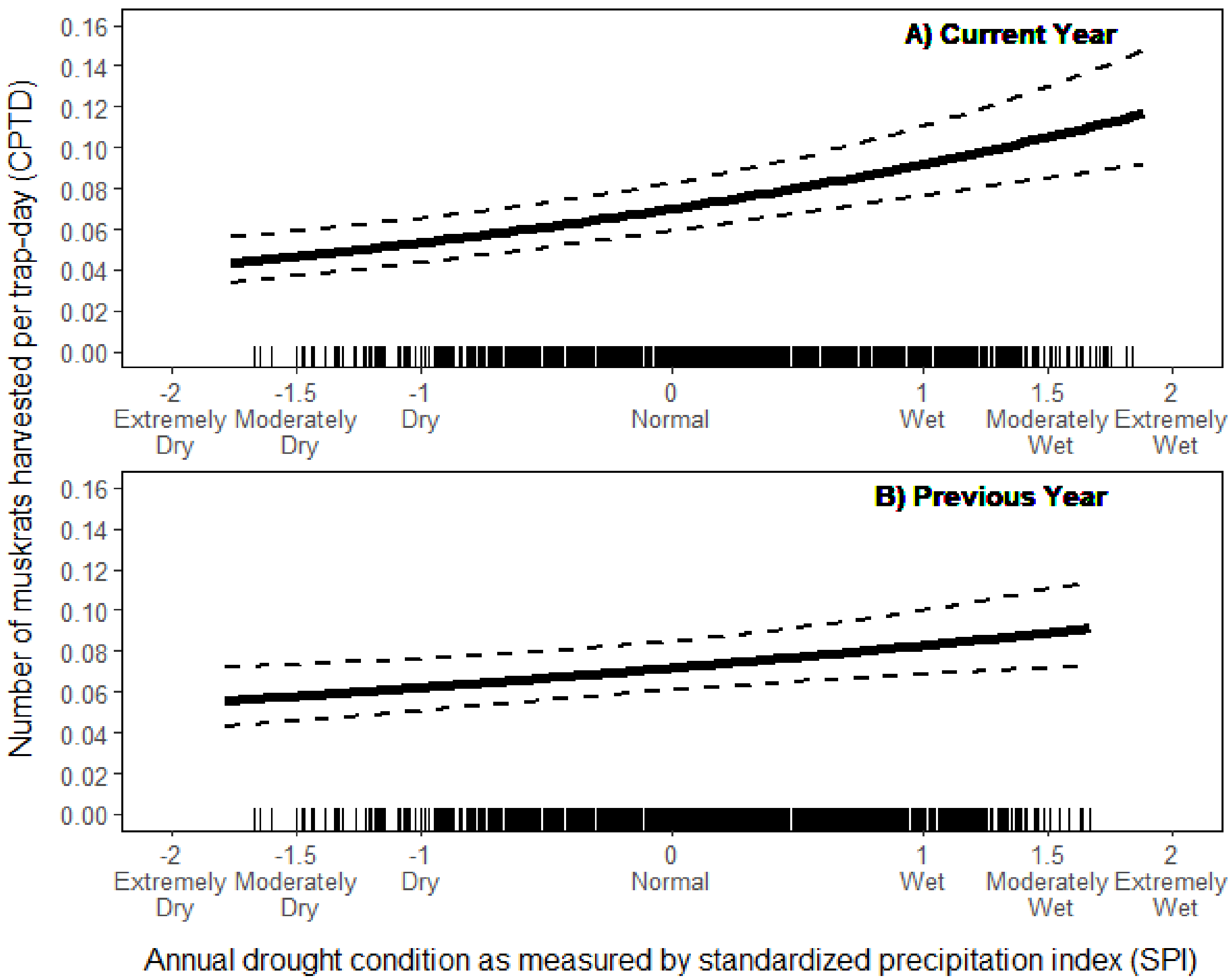


Fig. 6. Relationship between annual reported number of muskrats harvested per trap-day (CPTD) per county and drought conditions as measured by standardized precipitation index for A) the year in which harvest season was initiated (SPI_t) and B) the year preceding harvest season (SPI_{t-1}) based on furharvester survey data collected from 2010–2018 in Minnesota, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 51 models (Table 8, model 1) where all other model variables were held at their average value. Data included 1,021 county-harvest season combinations. Distribution of actual values for SPI_t or SPI_{t-1} are shown as a rug plot along the *x*-axis of each panel.

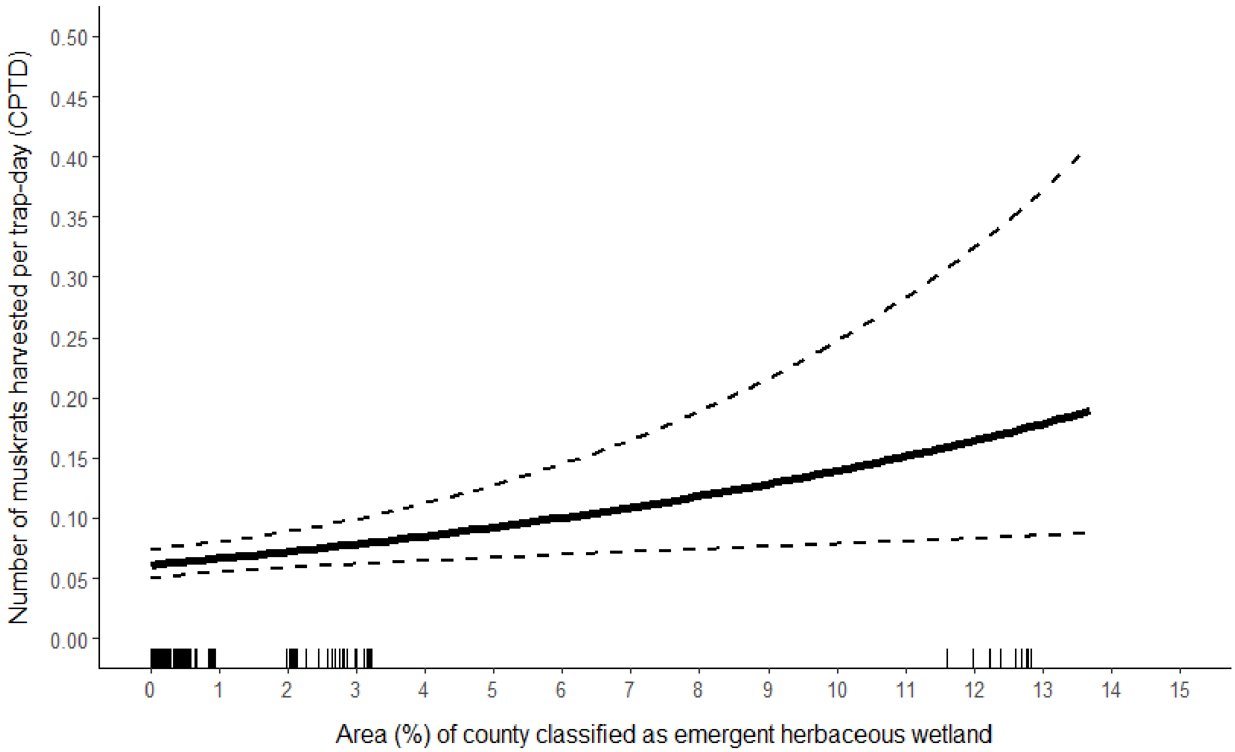


Fig. 7. Relationship between annual reported number of muskrats harvested per trap-day (CPTD) per county and area of emergent herbaceous wetlands (Area Emergent Wetlands) based on furharvester survey data collected from 2008–2018 in Ohio, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 54 models (Table 9, model 1) where all other model variables were held at their average value. Data included 763 county-harvest season combinations. Distribution of actual values for Area Emergent Wetlands are shown as a rug plot along the *x*-axis of each plot, respectively.

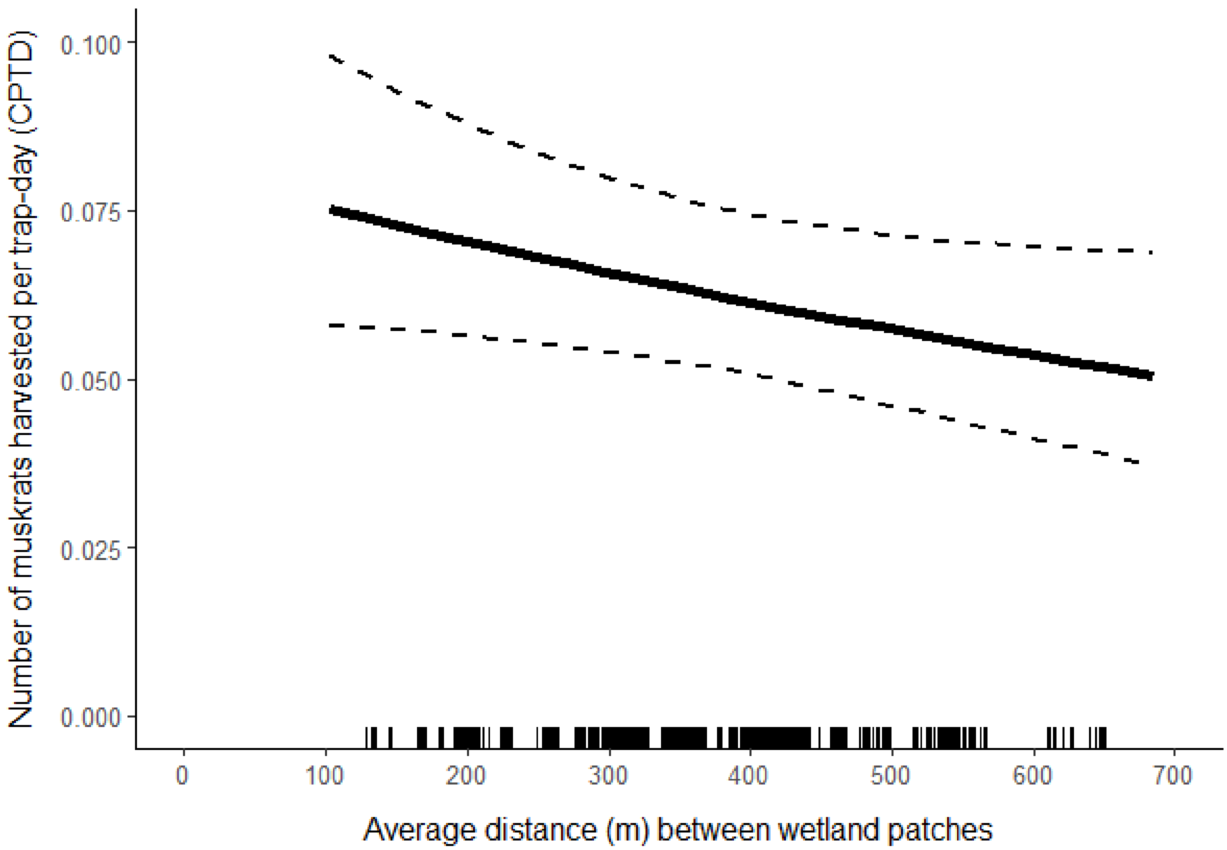


Fig. 8. Relationship between annual reported number of muskrats harvested per trap-day (CPTD) per county and average distance (m) between wetland patches (Connectivity) based on furharvester survey data collected from 2008–2018 in Ohio, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 54 models (Table 9, model 1) where all other model variables were held at their average value. Data included 763 county-harvest season combinations. Distribution of actual values for Connectivity are shown as a rug plot along the *x*-axis of each plot, respectively.

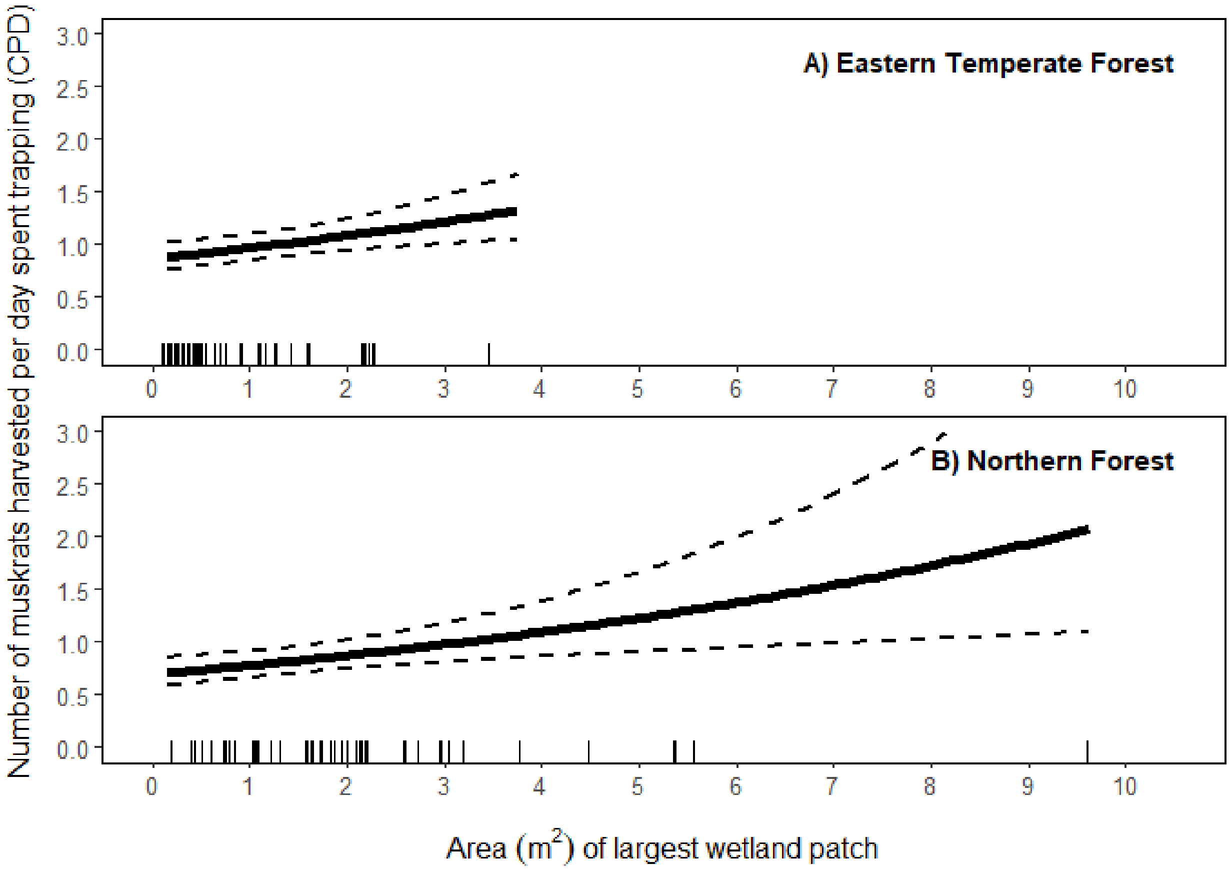


Fig. 9. Relationship between annual reported number of muskrats harvested per day spent trapping (CPD) per county and area (m^2) of the largest wetland patch per county (Largest Patch) for ecoregions A) Eastern Temperate Forest and B) Northern Forest based on furharvester survey data collected from 2010–2018 in Michigan, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 65 models (Table 10, model 1) where all other model variables were held at their average value. Data included 921 county-harvest season combinations. Distribution of actual values for Largest Patch are shown as a rug plot along the *x*-axis of each panel.

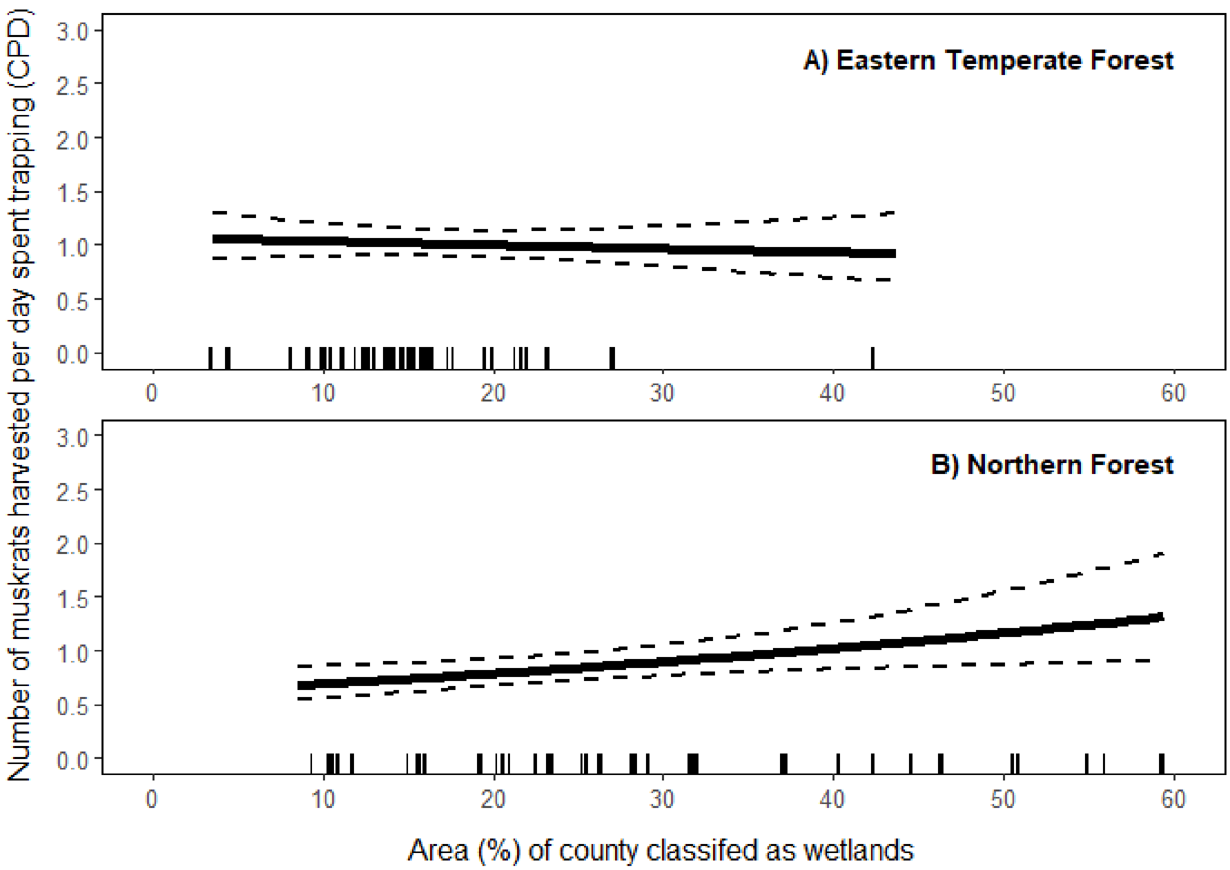


Fig. 10. Relationship between annual reported number of muskrats harvested per day spent trapping (CPD) per county and area (%) of wetlands (Area Wetlands) for ecoregions A) Eastern Temperate Forest and B) Northern Forest based on furharvester survey data collected from 2010–2018 in Michigan, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 65 models (Table 10, model 1) where all other model variables were held at their average value. Data included 921 county-harvest season combinations. Distribution of actual values for Area Wetlands are shown as a rug plot along the *x*-axis of each panel, respectively.

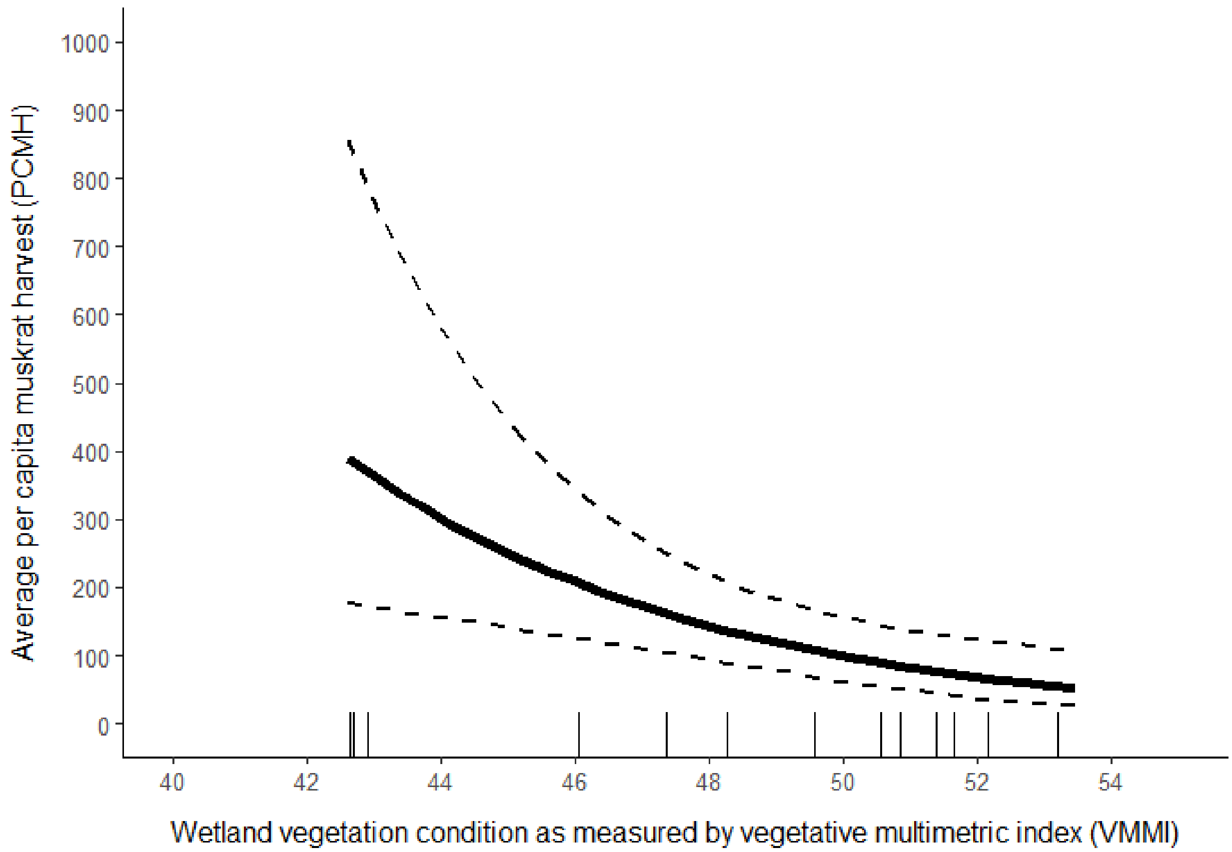


Fig. 11. Relationship between annual reported per capita muskrat harvest (PCMH) and wetland vegetation condition as measured by vegetative multimetric index (VMMI) for 7 national wildlife refuges and 6 state-managed areas distributed throughout the Great Lakes Basin, USA. Back-transformed relationship (solid lines) and 95% confidence interval (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 57 models where all other model variables were held at their average value. Data included 189 site-harvest season combinations. Distribution of actual values for VMMI are shown as a rug plot along the *x*-axis.

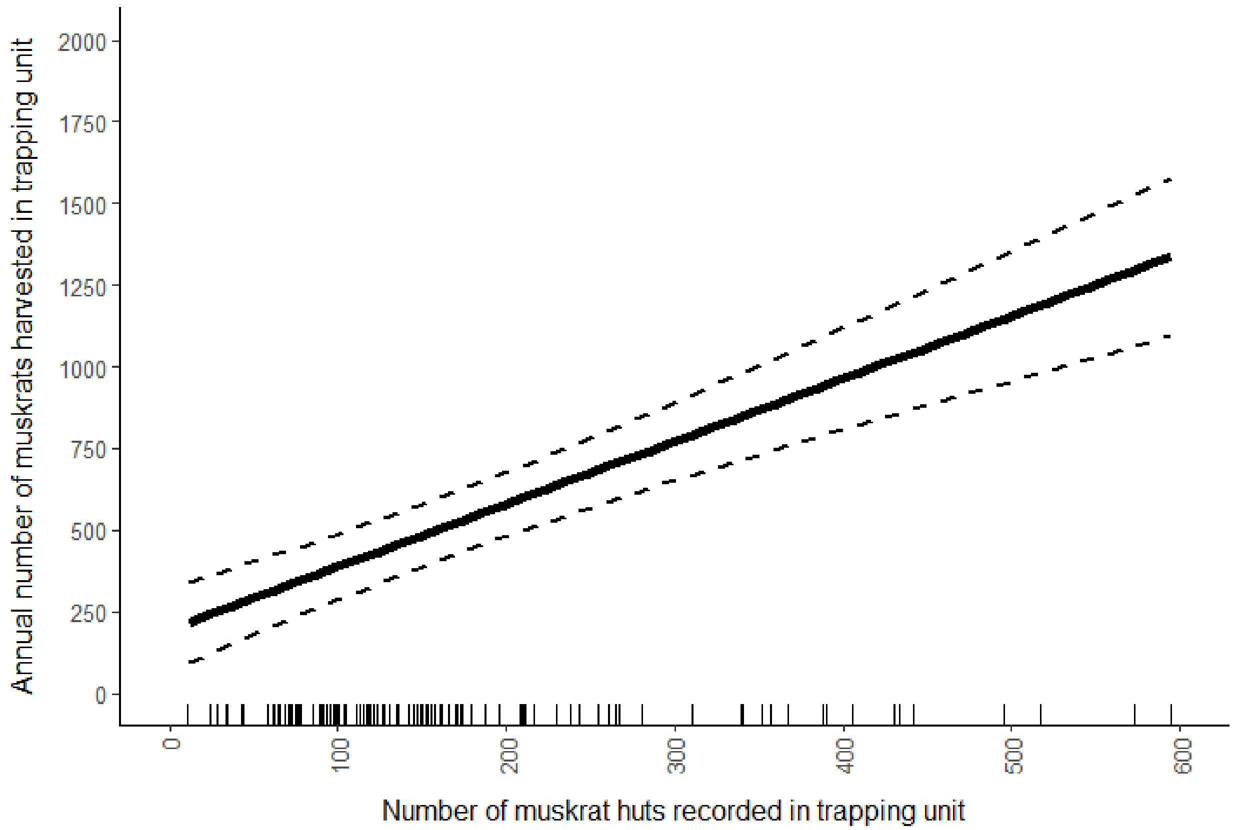


Fig. 12. Relationship between annual reported number of muskrats harvested per trapping unit and annual number of muskrat huts recorded per trapping unit collected at the Ottawa National Wildlife Refuge, Ottawa and Sandusky Counties, Ohio, USA, during 2001–2018. Back-transformed predicted relationship (solid line) and 95% confidence interval (dashed lines) were predicted from the best supported model based on Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). Data included 124 trapping unit-season combinations. Distribution of actual values for annual number of muskrat huts record within a trapping unit are shown as a rug plot along the *x*-axis.