

Empirical Evidence for Declines in Muskrat Populations Across the United States

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ABSTRACT Musk rats (*Ondatra zibethicus*) are native to North America and widely distributed across the continent. Recent evidence and anecdotal reports suggest that muskrat populations may be declining; however, this assumption has not been rigorously evaluated. We used 42 years of muskrat harvest data (1970–2012) from 37 states to examine trends in muskrat populations across the United States. Annual harvest data are highly correlated with annual pelt prices, which must be controlled for prior to analysis. After adjusting harvest data for the effects of current-year and 1-year-lagged pelt prices, we found strong support that muskrat populations have declined during this period. The slope of decline appeared stronger in the southeastern states and less pronounced in the midwestern states. Our results suggest that wildlife managers should consider active management programs for muskrat populations in regions where declines are observed. Along with recording annual muskrat harvest data, managers should also use rigorous surveys to identify changes in muskrat population abundances. Additionally, our study highlights the need for future research directed at revealing mechanistic explanations for synchronous muskrat declines across this large spatiotemporal scale. © 2017 The Wildlife Society.

KEY WORDS harvest, muskrat, *Ondatra zibethicus*, population decline, wetland.

Musk rats (*Ondatra zibethicus*) are an economically important furbearer species and are widespread throughout North America (Erb and Perry 2003). Studies on muskrat populations have shaped wildlife-management principles (Etrington 1961, 1963) and helped develop and test ecological hypotheses regarding trophic-level interactions (Erb et al. 2001, Haydon et al. 2009, Sundaram et al. 2013), population synchrony (Haydon et al. 2001, Estay et al. 2011), and the Moran effect (i.e., population synchrony across large spatial scales caused by an exogenous factor; Estay et al. 2011). Because muskrats also play vital ecosystem roles (Nyman et al. 1993, Connors et al. 2000) and are one of the most widely harvested furbearers in North America (White et al. 2015), wildlife managers require data on population abundances to inform management efforts. These data, however, are difficult to obtain over large spatial and temporal scales leaving biologists to rely on harvest data to track relative changes in population size. Harvest data likely reflect an interaction between animal abundance and trapper effort, including the number of trappers per year and how much time and work trappers invest in harvesting muskrats (Erickson 1982, Ahlers et al. 2016). Trapper effort may be influenced by economic

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factors (e.g., pelt price, gasoline prices) that must be identified and controlled during analysis (DeVink et al. 2011, McKelvey et al. 2011, Ahlers et al. 2016). Ahlers et al. (2016) reported that the annual number of muskrat trappers in Illinois, USA, a strong predictor of annual harvest, was related to pelt prices, gas prices, and unemployment rate during the trapping season. If economic incentives are related to harvest, investigators may infer spurious results about trends in muskrat populations that may lead to misleading ecological interpretations or misguided management decisions. In spite of this challenge, researchers have used uncorrected observations from fur harvest data to investigate many aspects of muskrat population ecology (Erb et al. 2001, Haydon et al. 2001, Holmengen et al. 2009, Sundaram et al. 2013). Roberts and Crimmins (2010) reported patterns in muskrat harvest data for 1986–2006 from 3 eastern Canadian provinces and 9 northeastern states in the United States that suggest a regional decline in muskrats but called for more extensive investigation of the decline. Declines in muskrat harvest over the past century have been reported in the United States (White et al. 2015), and anecdotal claims by trappers also support a decline in populations and distributions of United States harvest data over recent decades, however, comparing states and regions and controlling for economic correlates of harvest, has not been published. Without such an evaluation, wildlife managers can only speculate about the inferences made from state-specific annual harvest reports.



We investigated the empirical evidence for perceived muskrat population declines across the United States. If anecdotal reports are correct that muskrat populations are declining across the United States, we expect a statistically significant decline in state-specific annual muskrat harvest data (corrected for the economic influence of pelt prices) across our temporal sampling period. We also investigated for regional differences in potential declines across the United States. Finally, we suggest lines of inquiry we believe will be informative for interpreting and confirming population trends in muskrats and their causes.

STUDY AREA

Our study area included annual harvest data (1970–2012) for most of the contiguous United States (i.e., excluding AK, HI, and FL), which covers the southern half of the native geographic distribution of muskrats in North America. This region's climate and precipitation varies significantly by elevation, latitude, and longitude.

METHODS

Data

We obtained state-specific muskrat harvest data from 1970 to 2012 from the Association of Fish and Wildlife Associations' (AFWA) open-access database (http://www.fishwildlife.org/index.php?section=furbearer_management&activator=27).

State wildlife managers report annual species-specific harvest to AFWA and these data are compiled and presented online by AFWA managers. We acknowledge that there may have been differences in how individual states count and report harvest, but consistency in state-specific harvest reporting allowed analyses of within-state trends. A few states changed their trapping regulations during the time period examined, for example by banning body-gripping traps (CA, CO, MA, OK, WA). Some states did not report harvest data for long periods or reported harvest erratically, leaving gaps in the data that lowered our confidence in statistical analyses of population trends (AZ, ME, MD, MI, TX, WA). We included all states that reported harvest data in our maps summarizing patterns in muskrat harvest across the United States. We conducted statistical analyses of trends over time only for the subset of 37 states for which harvest data were consistently reported (Tables 1 and 2).

We initially attempted to obtain annual state-specific pelt price data by contacting state fish and wildlife agencies; however, the extent and completeness of these data varied across states. Annual pelt prices were highly correlated across the United States for 1970–2012 (Pearson correlation ≥ 0.93 for all pairwise comparisons among states for which we obtained pelt price data; Fig. 1) so we used the average annual pelt price from the 8 states for which we had the most complete information (IA, IL, IN, MN, NE, ND, AR, NC; Fig. 1). We corrected pelt prices for annual inflation by using the Consumer Price Index (CPI; www.bls.gov/data/), and adjusted all pelt prices to 2012 United States dollar values.

Data Analysis

To visualize the degree, direction, and generality of changes in raw harvest data over the 42 years we examined, we

compiled a map of the United States showing state-specific trends in muskrat harvest. For each state, we estimated the decline in harvest between the first half of our time series (1970–1990) and the second half (1991–2012). We calculated the percent decline as:

$$-\left(\bar{x}_{\text{harvest}_{1970-1990}} - \bar{x}_{\text{harvest}_{1991-2012}}\right) / \bar{x}_{\text{harvest}_{1970-1990}}.$$

This division also seemed appropriate because the most dramatic declines in harvest occurred around 1990. Observed declines in muskrat harvest during 1990 may partially be due to concurrent economic changes in the fur market. We could not calculate the percent decline for Arizona and Maine because these states did not report muskrat harvest data after 1990, and harvest from Texas was reported for too few years (only 14 of 41) and none since 2000. We also conducted linear regressions of ln-transformed harvest data versus year for each state (PROC REG; SAS[®] version 9.4, SAS Institute, Cary, North Carolina, USA) to evaluate the direction of harvest trends from 1970 to 2012. Finally, we grouped states by AFWA-defined regions (Southeast, Northeast, Midwest, West; Tables 1 and 2) to examine potential regional differences in declines in muskrat harvest. Before summing harvest data from states within each region, however, we had to extrapolate missing data to minimize obscuring trends because different numbers of states contributed data in different years (Fig. S1, available online in Supporting Information). To estimate harvest for a state missing data for year x , we calculated the proportional change between year $x - 1$ and year x for all other states in that region and multiplied that value by the harvest in year $x - 1$ for the focal state. We preferred this method to a simple mean of harvest between years $x - 1$ and $x + 1$ because it was more likely to conserve any regional annual change (i.e., was more consistent with changes shown by other states in the region). We did not include states missing data for gaps > 3 years. States compiled in each region included Southeast (AL, AR, GA, KY, LA, NC, SC, TN, VA, WV), Northeast (CT, DE, MA, NH, NJ, NY, PA, RI), Midwest (IA, IN, MN, OH, MO, KS, NE, ND, SD, WI), and West (CA, ID, MT, NV, NM, OK, OR, UT, WY). We then evaluated declines in ln-transformed regional annual harvest by linear regression (PROC REG; SAS[®] version 9.4).

We used generalized linear models (PROC GENMOD; SAS[®] version 9.4) to assess annual trends in ln-transformed muskrat harvest data (Harvest) while simultaneously controlling for the effects of current-year and 1-year-lagged pelt prices. Harvest data may be influenced by pelt prices for the current trapping year or by pelt prices the previous year. For each state, we constructed 4 models that used different methods to control for CPI-adjusted pelt price (Pelt). First, we constructed models for each state that included year (Yr) and current-year pelt price (Harvest = Yr + Pelt) and a model including a 1-year lag in pelt prices (Harvest = Yr + LagPelt). Second, we created state-specific models that divided annual muskrat harvest by the current-year CPI-adjusted pelt price for that specific year (AdjHarvest = Yr) and a similar model that also incorporated a 1-year time lag (LagAdjHarvest = Yr). This method has been used in other

Table 1. State-specific model statistics explaining variation in annual muskrat harvest from 1970 to 2012 while controlling for the effect of inflation-adjusted pelt prices. We grouped states in ecoregions previously defined by the American Fish and Wildlife Association. For each state, we controlled for the effect of pelt price differently in 2 separate linear models (Harvest = Yr + Pelt; AdjHarvest = Yr). Harvest = reported muskrat harvest for a particular season, AdjHarvest = reported muskrat harvest divided by the inflation-adjusted pelt price for that season, Yr = year of fur-harvest season, Pelt = inflation-adjusted muskrat pelt price for a particular fur-harvest season. We derived beta estimates, standard errors, and *P*-values from generalized linear models and estimates represent the year covariate for both models.

Ecoregion	State	Harvest = Yr + Pelt			AdjHarvest = Yr		
		β	SE	<i>P</i>	β	SE	<i>P</i>
Southeast	AL	-0.0339	0.0165	0.040	-0.0604	0.0121	≤0.001
	AR	-0.0996	0.0133	≤0.001	-0.0850	0.0108	≤0.001
	GA	-0.0562	0.0108	≤0.001	-0.0616	0.0079	0.370
	KY	-0.0864	0.0105	≤0.001	-0.0693	0.0081	≤0.001
	LA	-0.2096	0.0158	≤0.001	-0.2011	0.0121	≤0.001
	MS	-0.1008	0.0067	≤0.001	-0.1007	0.0048	≤0.001
	NC	-0.0846	0.0194	≤0.001	-0.0767	0.0139	≤0.001
	SC	-0.0706	0.0154	≤0.001	-0.0323	0.0129	0.012
	TN	-0.1115	0.0109	≤0.001	-0.0904	0.0090	≤0.001
	VA	-0.0773	0.0080	≤0.001	-0.0633	0.0096	≤0.001
Midwest	WV	-0.0628	0.0094	≤0.001	-0.0550	0.0071	≤0.001
	IL	-0.0792	0.0062	≤0.001	-0.0580	0.0046	≤0.001
	IN	-0.0401	0.0081	≤0.001	-0.0261	0.0065	≤0.001
	IA	-0.0510	0.0052	≤0.001	-0.0248	0.0041	≤0.001
	KS	-0.0003	0.0115	0.978	0.0046	0.0079	0.560
	MN	-0.0351	0.0112	0.002	-0.0136	0.0083	0.102
	MO	-0.0423	0.0154	≤0.001	-0.0258	0.0102	≤0.001
	NE	-0.0274	0.0107	0.002	-0.0084	0.0071	0.222
	ND	0.0242	0.0050	0.349	0.0171	0.0041	0.370
	OH	-0.0725	0.0046	≤0.001	-0.0423	0.0062	≤0.001
West	SD	-0.0056	0.0266	0.833	-0.0040	0.0193	0.831
	WI	-0.0037	0.0058	0.691	0.0116	0.0045	0.103
	ID	-0.0490	0.0065	≤0.001	-0.0336	0.0058	≤0.001
	MT	-0.0095	0.0052	0.066	-0.0016	0.0041	0.707
	NV	-0.0350	0.0258	0.071	-0.0402	0.0190	0.004
	NM	-0.1226	0.0053	≤0.001	-0.1029	0.0060	≤0.001
	OR	-0.0430	0.0067	≤0.001	-0.0221	0.0061	≤0.001
	UT	-0.0652	0.0128	≤0.001	-0.0118	0.0134	0.381
	WY	-0.0025	0.0151	0.870	-0.0052	0.0113	0.645
	Northeast	CT	-0.0678	0.0070	≤0.001	-0.0701	0.0075
DE		-0.0301	0.0079	≤0.001	-0.0071	0.0079	0.370
NH		-0.0447	0.0090	≤0.001	-0.0219	0.0069	≤0.001
NJ		-0.0729	0.0053	≤0.001	-0.0468	0.0061	≤0.001
NY		-0.0267	0.0164	≤0.001	-0.0142	0.0121	0.001
PA		-0.0408	0.0040	≤0.001	-0.0131	0.0063	0.037
RI		-0.0873	0.0074	≤0.001	-0.0630	0.0075	≤0.001
VT	-0.0695	0.0063	≤0.001	-0.0540	0.0044	≤0.001	

studies that attempted to control for the influence of pelt prices on estimates of population trends from harvest data (Gosselink et al. 2003). We assumed that controlling for pelt prices would provide reasonable indices for muskrat availability (e.g., population abundance) for a given year (Ahlers et al. 2016). We determined the potential for state-specific muskrat population declines by assessing beta estimates for the year variable in all models. For all models that had negative beta estimates (with standard errors that did not overlap 0), we assumed muskrat populations declined within that particular state over our study period. For positive beta estimates (with standard errors that did not overlap 0), we assumed muskrat populations increased in that state over our study period.

To visualize patterns in potential declines in muskrat abundance based on harvest after controlling for pelt price, we used the multiple regression models to generate predicted values of annual harvest for each year in each state holding

current-year pelt price constant, then constructed a second map of the United States showing declines in mean harvest between 1970–1990 and 1991–2012 using the same method used for raw harvest data.

RESULTS

From 1970 to 2012, AFWA reported 132,057,218 muskrats were harvested from the 37 states included in our study (annual median = 1,890,337; range = 731,486–8,106,786). Average annual state-specific muskrat harvest ($n = 37$) varied widely across years ($\bar{x} = 85,955 \pm 166,482$ [SD]). Because some states did not report estimated muskrat harvests to AFWA every year, these numbers underestimate the true muskrat harvest during our study.

Muskrat harvest declined dramatically between 1970–1990 and 1991–2012 throughout the United States (Fig. 2). Declines in state-specific harvest were greatest in the

Table 2. State-specific model statistics explaining variation in annual muskrat harvest from 1970 to 2012 while controlling for the effect of a 1-year lag in inflation-adjusted pelt prices. We grouped states in ecoregions previously defined by the American Fish and Wildlife Association. For each state, we controlled for the effect of a 1-year lag in muskrat pelt price in 2 separate linear models ($\text{Harvest} = \text{Yr} + \text{LagPelt}$; $\text{LagAdjHarvest} = \text{Yr}$). Harvest = reported muskrat harvest for a particular season, LagAdjHarvest = reported muskrat harvest for a particular season divided by the inflation-adjusted pelt price from the previous season, Yr = year of fur-harvest season, Pelt = inflation-adjusted muskrat pelt price for a particular fur-harvest season, LagPelt = inflation-adjusted muskrat pelt price from the previous fur-harvest season. We derived beta estimates, standard errors, and P -values from generalized linear models and estimates represent the year covariate for all models.

Ecoregion	State	Harvest = Yr + LagPelt			LagAdjHarvest = Yr		
		β	SE	P	β	SE	P
Southeast	AL	-0.0337	0.0187	0.071	-0.0535	0.0137	≤ 0.001
	AR	-0.0992	0.0118	≤ 0.001	-0.0890	0.0091	≤ 0.001
	GA	-0.0612	0.0115	≤ 0.001	-0.0653	0.0085	≤ 0.001
	KY	-0.0891	0.0102	≤ 0.001	-0.0714	0.0078	≤ 0.001
	LA	-0.2008	0.0155	≤ 0.001	-0.1976	0.0114	≤ 0.001
	MS	-0.0892	0.0136	≤ 0.001	-0.0940	0.0092	≤ 0.001
	NC	-0.0782	0.0117	≤ 0.001	-0.0714	0.0081	≤ 0.001
	SC	-0.0730	0.0098	≤ 0.001	-0.0464	0.0082	≤ 0.001
	TN	-0.1114	0.0092	≤ 0.001	-0.0896	0.0075	≤ 0.001
	VA	-0.0760	0.0071	≤ 0.001	-0.0614	0.0060	≤ 0.001
	WV	-0.0661	0.0066	≤ 0.001	-0.0587	0.0051	≤ 0.001
Midwest	IL	-0.0735	0.0080	≤ 0.001	-0.0533	0.0066	≤ 0.001
	IN	-0.0418	0.0059	≤ 0.001	-0.0285	0.0048	≤ 0.001
	IA	-0.0527	0.0063	≤ 0.001	-0.0294	0.0064	≤ 0.001
	KS	-0.0062	0.0124	0.620	0.0017	0.0093	0.852
	MN	-0.0313	0.0112	0.005	-0.0151	0.0081	0.063
	MO	-0.0416	0.0072	≤ 0.001	-0.0271	0.0053	≤ 0.001
	NE	-0.0285	0.0088	0.001	-0.0127	0.0066	0.056
	ND	0.0340	0.0261	0.193	-0.0226	0.0192	0.239
	OH	-0.0745	0.0045	≤ 0.001	-0.0469	0.0065	≤ 0.001
	SD	-0.0120	0.0249	0.632	-0.0045	0.0182	0.803
	WI	-0.0051	0.0095	0.592	0.0080	0.0071	0.256
West	ID	-0.0457	0.0066	≤ 0.001	-0.0319	0.0053	≤ 0.001
	MT	-0.0083	0.0052	0.115	-0.0001	0.0045	0.980
	NV	-0.0289	0.0193	0.134	-0.0375	0.0143	0.009
	NM	-0.1256	0.0150	≤ 0.001	-0.1029	0.0122	≤ 0.001
	OR	-0.0456	0.0069	≤ 0.001	-0.0230	0.0068	0.001
	UT	-0.0634	0.0138	≤ 0.001	-0.0188	0.0135	0.164
	WY	-0.0075	0.0014	0.594	0.0023	0.0105	0.824
Northeast	CT	-0.0571	0.0084	≤ 0.001	-0.0565	0.0089	≤ 0.001
	DE	-0.0288	0.0074	≤ 0.001	-0.0092	0.0077	0.229
	NH	-0.0436	0.0045	≤ 0.001	-0.0240	0.0054	≤ 0.001
	NJ	-0.0728	0.0046	≤ 0.001	-0.0488	0.0052	≤ 0.001
	NY	-0.0246	0.0059	≤ 0.001	-0.0111	0.0048	0.022
	PA	-0.0423	0.0041	≤ 0.001	-0.0132	0.0061	0.030
	RI	-0.0783	0.0068	≤ 0.001	-0.0609	0.0065	≤ 0.001
	VT	-0.0673	0.0081	≤ 0.001	-0.0447	0.0107	≤ 0.001

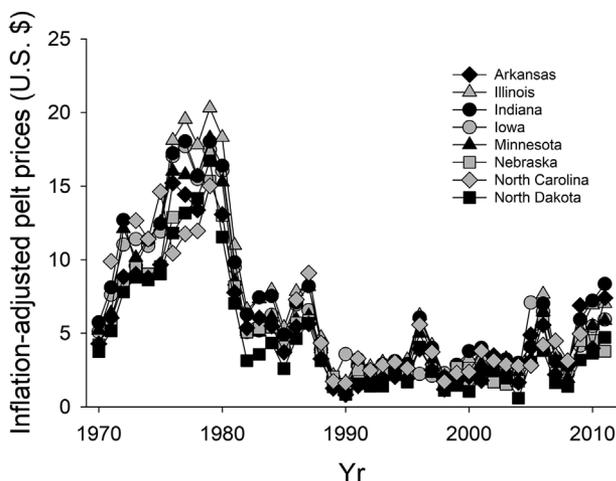


Figure 1. Temporal trends and correlation in muskrat pelt prices from 8 states within the United States between 1970 and 2012.

southern states, often showing a decline of $>90\%$ between the first half and second half of the period evaluated. Overall, declines in harvest over time were significant ($P < 0.05$) in all states except North and South Dakota (Fig. S1). Declines in harvest also were significant for each region (Southeast: $\beta = -0.1186 \pm 0.0076$ [SE], $P \leq 0.001$; Northeast: $\beta = -0.0503 \pm 0.0040$, $P \leq 0.001$; Midwest: $\beta = -0.0440 \pm 0.0059$, $P \leq 0.001$; West: $\beta = -0.0556 \pm 0.0054$, $P \leq 0.001$; Fig. 3), with the greatest declines in the Southeast.

After controlling for the effects of current-year ($\text{Harvest} = \text{Yr} + \text{Pelt}$) and 1-year-lagged pelt prices ($\text{Harvest} = \text{Yr} + \text{LagPelt}$), all 11 states in the Southeast region (10 of 11 with 1-yr-lag model), all states in the Northeast region, 7 of 11 states in the Midwest region, and 4 of 7 states in the West region exhibited population declines based on estimates from the multiple regression models (Fig. 4A; Tables 1 and 2). Ten of 11 states in the Southeast region, 7 of 8 states in the

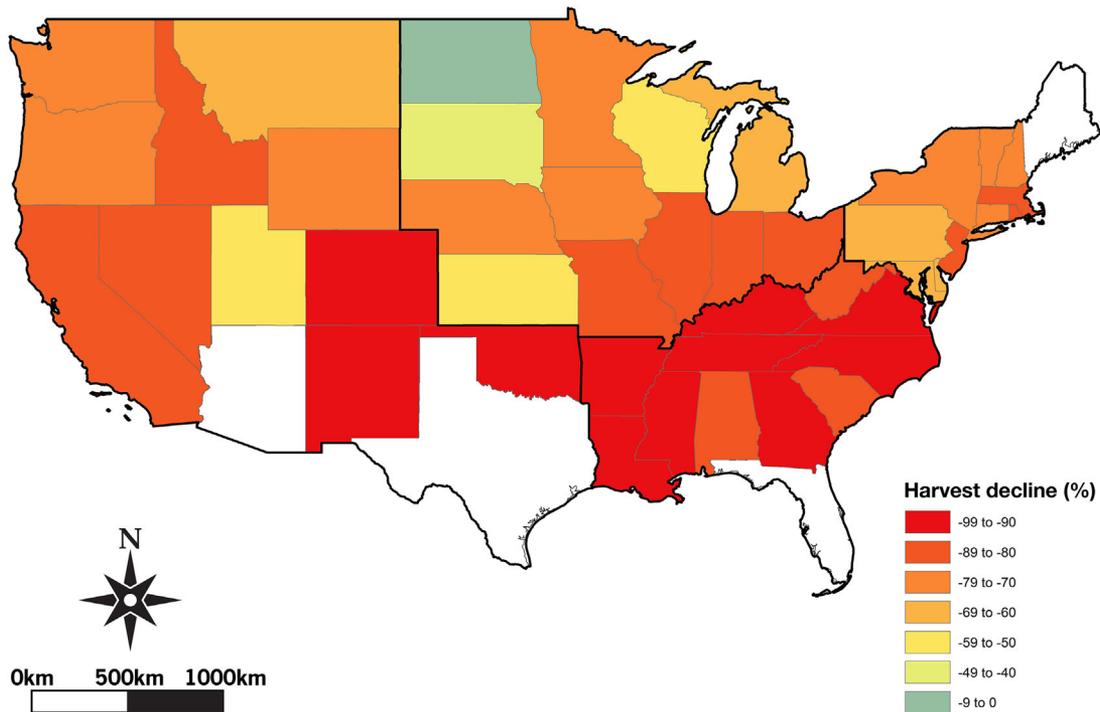


Figure 2. Percent decline in muskrat harvest by fur trappers between 1970–1990 and 1991–2012 in the contiguous United States (we excluded AZ, ME, and TX because of incomplete harvest data across these time periods). We calculated percent decline as $-(\bar{x} \text{ harvest}_{1970-1990} - \bar{x} \text{ harvest}_{1991-2012}) / \bar{x} \text{ harvest}_{1970-1990}$.

Northeast region, 5 of 11 states in the Midwest region, and 4 of 7 states in the West region exhibited population declines based on estimates from the models based on AdjHarvest and LogAdjHarvest (Fig 4B; Tables 1 and 2). Some states showed an increase in muskrat harvest with current-year (ND and WI) and 1-year-lag pelt price models (KS, ND, and WY); however, the *P* values associated with all model estimates were not significant (Tables 1 and 2).

After controlling for current-year pelt price, the decrease in predicted mean harvest between 1970–1990 and 1991–2012

was much less dramatic than that in raw mean harvest for most states (Fig. 5) but remained greatest in the southern and some eastern states. A few states in the Midwest (ND, SD, MI, WI, KS) and West (WY, MT) showed no or only modest declines after controlling for pelt price (Fig. 5).

DISCUSSION

Our analyses provide supportive evidence that muskrat abundances have declined across much of the United States since 1970. Even after controlling for the effects of current-year and lagged pelt prices, the majority of states showed significant declines in muskrat harvest, which likely reflect a declining trend in muskrat availability. Harvest data for some states include gaps in reporting (Fig. S1), changes in trapping regulations, or generally low numbers; thus, quantitative values for trends for individual states should be considered with caution. A few geographic patterns emerge, however. Declines in harvest were greatest in southern states, some lower midwestern states, and many northeastern states, even after controlling for pelt price. However, controlling for pelt prices with multiple methods revealed that declines in predicted harvest were not as evident in some upper midwestern and western states.

Our analyses confirm observations of declines by trappers and managers (Roberts and Crimmins 2010). Confirmation that declines in harvest actually correspond to declines in muskrat availability is sorely needed. The minimum spatial scale of our data (e.g., state) likely masks small-scale spatial and temporal variability in muskrat abundance and distribution within each state. However, the widespread

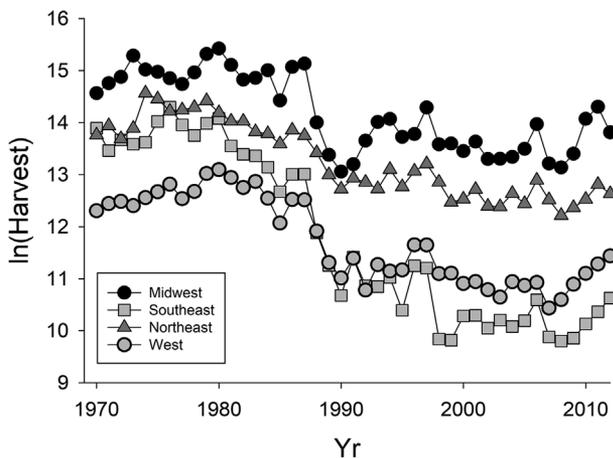


Figure 3. Natural log-transformed trends in muskrat harvest (1970–2012) in 4 regions of the United States defined by the Association of Fish and Wildlife Associations.

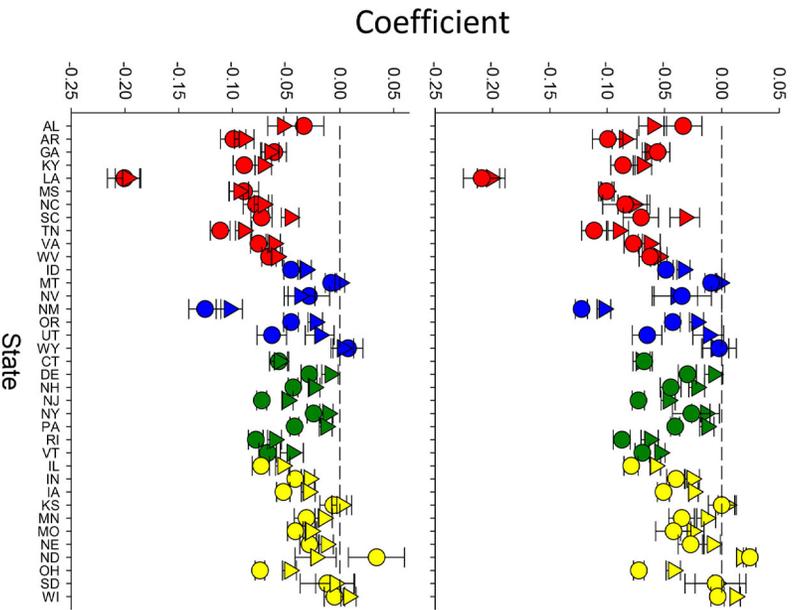


Figure 4. State-specific annual trend analysis (1970–2012) of muskrat harvest data spanning 37 states and 4 regions (red = Southeast, blue = Western, green = Northeast, yellow = Midwest). We controlled for the strong effect of pelt prices using 2 models that incorporated average current-year pelt prices (top) and 2 models incorporating 1-year-lagged pelt prices (bottom). Circles represent beta estimates and standard errors from the year variable in models that divided annual muskrat harvest by current-year pelt price ($\text{AdjHarvest} = \text{Yr}$) and 1-year lag in pelt prices ($\text{LogAdjHarvest} = \text{Yr}$). Triangles represent beta estimates and standard errors from the year variable in models that controlled for current-year pelt prices ($\text{Harvest} = \text{Yr} + \text{Pelt}$) and a 1-year lag in pelt prices ($\text{Harvest} = \text{Yr} + \text{LagPelt}$). Coefficient = beta estimate (and SE) of the year covariate and was derived from a generalized linear model. Estimates < 0.00 indicate population decline, whereas estimates > 0.00 indicate population growth.

geographic distribution of declines in muskrat harvest suggests a general underlying cause. Regional differences (e.g., Southeast vs. upper Midwest) in the degree of declines suggest that there is variation in this underlying cause, or that muskrat harvest is affected by state-specific factors. Geographic comparisons of muskrat density and distribution within and among states could supplement historical data to evaluate factors affecting population trends and the relationship between statewide harvest data and true population declines. Although we did not attempt to uncover a mechanistic explanation for these possible declines in the present study, we present 5 plausible (and testable) hypotheses: habitat loss or isolation, habitat degradation, changing hydrology, predation and competition, and a shifting fur-harvest culture hypothesis.

Habitat Loss or Isolation Hypotheses

Wetland loss is persistent in the United States (Suloway and Hubbell 1994, McCauley and Jenkins 2005, Zedler and

Kercher 2005, Miller et al. 2009) and a possible explanation for suspected muskrat population declines. Muskrats are wetland obligates (Wilner et al. 1980) and require wetlands for food resources, reproduction, predator avoidance, and shelter (Errington 1963). Thus, reduced muskrat harvest could reflect reduced statewide abundances as a consequence of loss of total area of good-quality wetlands.

Reduced connectivity of remaining good-quality wetlands may explain potential muskrat population declines. Dispersal capability of muskrats is limited (Errington 1963) and is dependent on matrix habitat quality (Schooley and Branch 2009, Laurence et al. 2013). Thus, functional connectivity among populations is important for maintaining immigration and preventing local population extinctions (MacArthur and Wilson 1963, Hanski 1999). Wetland loss can increase the geographic distance between good-quality wetlands (McCauley and Jenkins 2005), reducing the probability of colonization or altering metapopulation dynamics for semiaquatic species (Jenkins et al. 2001).

Habitat Degradation Hypothesis

Physical degradation of remaining wetlands could have a direct or indirect effect on muskrat population growth. Wetlands are subject to invasive and hybrid plant invasions (Spyreas et al. 2009, Travis et al. 2010, Travis et al. 2011), pathogen transmission (Shapiro et al. 2010, Ahlers et al. 2015*b*), and fluctuating water levels (King et al. 2009, Farrell et al. 2010), which may all have the potential to affect muskrat population persistence. Anthropogenic landscape change (e.g., urbanization, channelization, tile drainage in agricultural systems) can cause increased rates of flooding in some areas (King et al. 2009, Ahlers et al. 2010). Exposure to pesticides, herbicides, or pharmaceuticals from surrounding human-modified landscapes has been shown to negatively affect aquatic and semiaquatic communities (Solomon et al. 1996, Relyea 2009, Vazquez-Roig et al. 2012) and can likely affect muskrat populations.

Changing Hydrology Hypothesis

Climate change is affecting wetland hydrology because of the increasing frequency of extreme precipitation and drought events (Easterling et al. 2000, Dai 2013). Increased amounts of rainfall in some storms due to climate change could exacerbate changes in hydrology because of landscape alteration. Muskrats may be negatively affected by extreme fluctuations in hydrology (Ahlers et al. 2015*a*) because low water levels can expose burrows to predators (Errington 1943) and flooding can negatively affect kit survival (Kinler et al. 1990). In areas of the Midwest many wetlands have been drained and most available muskrat habitat occurs in agricultural ditches. These habitats are exposed to extreme water-level fluctuations which may affect muskrat population growth. Additionally, artificial water-level regulation may affect muskrat abundances in wetlands (Greenhorn et al. 2017).

Predation and Competition Hypotheses

Although American mink (*Neovison vison*) are considered the main predator of muskrats, muskrats are susceptible to a suite of other predator species (Willner et al. 1980). Coyotes

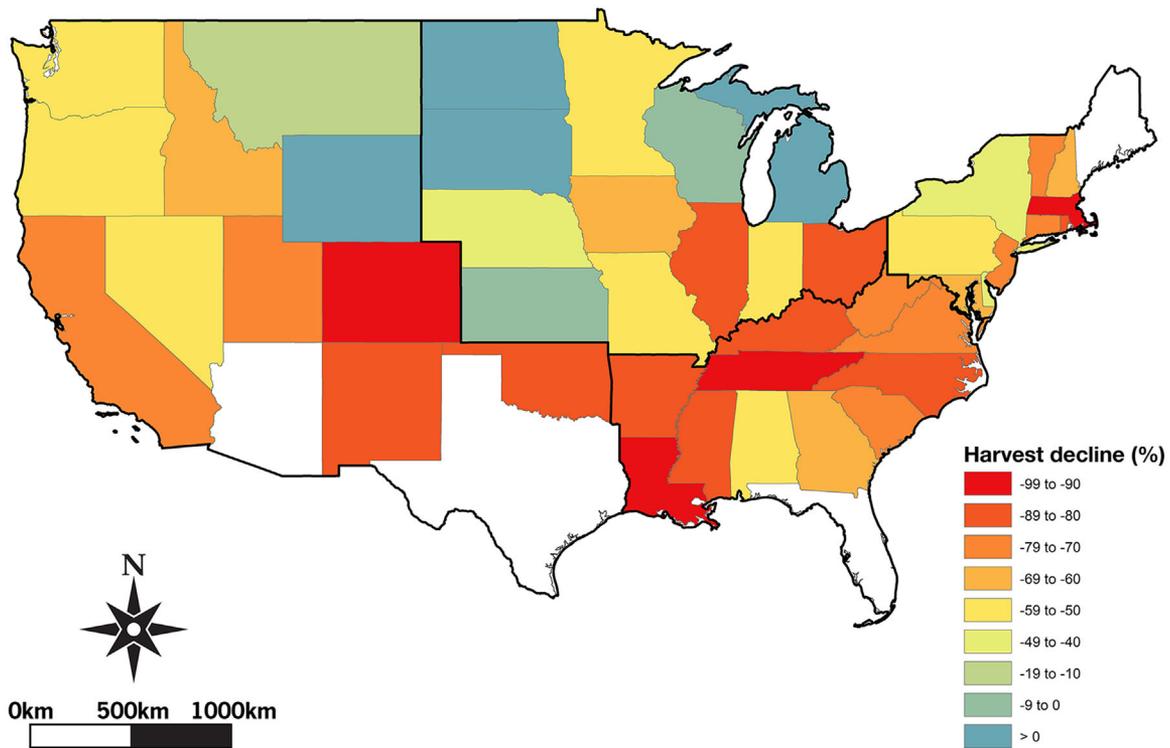


Figure 5. Percent decline in predicted muskrat harvest by fur trappers between 1970–1990 and 1991–2012, after controlling for the effect of pelt price in the contiguous United States (we excluded AZ, ME, and TX because of incomplete harvest data across these time periods). We calculated percent decline as $-(\bar{x} \text{ predicted harvest}_{1970-1990} - \bar{x} \text{ predicted harvest}_{1991-2012}) / \bar{x} \text{ predicted harvest}_{1970-1990}$. We adjusted annual pelt prices for inflation to 2012 U.S. dollars.

(*Canis latrans*) and bald eagles (*Haliaeetus leucocephalus*) are predators of muskrats (Errington 1963, Dunstan and Harper 1975, Ahlers et al. 2010), and raccoons (*Procyon lotor*) are predators of muskrat kits (Dorney 1954). These predator species have been increasing in abundance (some exponentially) or expanding their distribution across the United States (Zevloff 2002, Gosselink et al. 2003, Jenkins and Sherrod 2005, Watts et al. 2008) and therefore may have an increasing impact on muskrat populations.

To our knowledge, competition between muskrats and other semiaquatic mammals has not been investigated. However, nutria (*Myocastor coypus*), a larger semiaquatic herbivore, have been introduced to some states along the Gulf of Mexico, southern and mid-Atlantic coast, and Pacific Northwest. Nutria feed primarily on marsh and wetland plants, sometimes degrading muskrat habitat and even causing loss of marshes (Evers et al. 1998, Shaffer et al. 2015). Nutria are also larger than muskrats, and could displace them (Boscarenno 2009).

Shifting Fur-Harvesting Culture Hypothesis

Muskrat harvest data since 1970 are strongly related to economic incentives, particularly pelt prices, in Illinois (Ahlers et al. 2016), and likely elsewhere in North America (Roberts and Crimmins 2010). Many studies have used harvest data to describe and interpret muskrat population trends in Canada without controlling for pelt price (Elton and Nicholson 1942, Erb et al. 2000, Holmengen et al. 2009), and have been influential in our understanding of

predator-prey dynamics (Erb et al. 2001, Haydon et al. 2001) and spatial variation in population cycling (Erb et al. 2000, Estay et al. 2011). However, the Hudson's Bay Company harvest data from 1925 to 1949 may be less subject to economic bias; trappers in Canada during that time period may have relied on fur trapping for their livelihood and gave trapping their full effort each year regardless of pelt price (Viljugrein et al. 2001). Similar sampling effort (i.e., muskrat trapping) among years could allow harvest data to reflect changes in muskrat abundance. Even after controlling for pelt price, however, decreasing annual trapper effort in the United States from 1970 to 2012 could have resulted from a variety of cultural and social changes.

Muskrat trapping may have become more of a recreational activity than an essential source of income in recent decades, and trapper effort thus may be more responsive to economic incentives. Fur trapping may be waning as a cultural tradition in some areas; as older trappers leave the population, their replacement rate by new recruits into the trapping tradition may be decreasing (Ahlers et al. 2016). Lower pelt prices in recent decades partly reflects less demand by a society that has shifted its attitude away from appreciation of fur products; this value shift also may discourage new recruits into fur trapping. Finally, access to trapping areas could decrease not only through habitat loss or degradation but through limitations imposed by private property owners whose attitudes have shifted from a utilitarian perspective to a conservation perspective that does not include fur harvest. These and other social factors that could be correlated with

declines in muskrat harvest should be investigated through human dimensions research.

Our study is the first to investigate and report long-term muskrat population trends across the continuous United States. Although historical studies of muskrat population dynamics have shaped our broader understanding of ecological processes (Errington 1963), we have a limited understanding of trajectories in muskrat population abundances. This is concerning because many anecdotal reports concur that muskrat abundances are declining across the United States. Future studies should focus on obtaining robust and comparable estimates of muskrat population sizes across their geographic distribution. Smaller-scale studies investigating muskrat population responses to wetland loss, isolation, and degradation are also timely and warranted.

MANAGEMENT IMPLICATIONS

Management of muskrat populations has mostly centered on eradication or removal of nuisance populations. These efforts are justifiable because dams and retention ponds can incur costly damage due to muskrat burrowing activities. Managers, however, should also identify wetlands where conservation or restoration efforts of muskrat populations will not interfere with public infrastructure, and actively manage harvest thresholds or restoration of populations in these areas. We recommend that researchers develop and initiate long-term studies of muskrat abundance trends using statistically sound and unbiased sampling methods. These studies will likely be costly and require long-term commitments from multiple agencies to be successful. As such, regional collaborations of resources will be necessary. Additionally, we recommend regional cooperation in study design, data collection, and data management so resulting trends are comparable and data-collection methods are easily replicated elsewhere.

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