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Research Article

Identifying and Controlling for Variation in Canid Harvest Data

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ABSTRACT An accurate understanding of harvest trends is required for effective wildlife management. Trapper harvest data represent valuable long-term data for evaluating patterns and trends for wildlife species at broad spatiotemporal scales. Inferring accurate trends from harvest data, however, first requires identifying and controlling for confounding factors that vary independent of abundance. We investigated trends in 43 years of trapper harvest data (1976–2018) from Illinois, USA, for red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), and coyote (*Canis latrans*) while controlling for factors that may affect trapper effort, including number of effective (i.e., successful) trappers, pelt price, gasoline price, winter unemployment, and winter weather conditions. Annual trapper harvest for red and gray foxes declined and was affected by gasoline price and winter unemployment, whereas annual trapper harvest for coyotes increased and was not strongly affected by other covariates. After adjusting for pelt price, harvest of red foxes was relatively stable, but harvest of gray foxes declined and harvest of coyotes increased. Effects of covariates on harvest per successful trapper varied by species; nevertheless, we detected an increasing trend for coyotes and decreasing trends for gray foxes and red foxes. Concordance across indices for gray foxes and coyotes was consistent with hypothesized declines for gray foxes and increases for coyotes in the midwestern United States. Trends for red foxes varied depending on how we accounted for potential confounding factors and it is unclear if these trends suggest population declines or distribution shifts to urban areas with reduced trapping susceptibility. Our results highlight the importance of understanding sources of variation in harvest data and that their effects can vary across species.

KEY WORDS *Canis latrans*, coyote, gray fox, Illinois, pelt price, red fox, trapper effort, trapper harvest, *Urocyon cinereoargenteus*, *Vulpes vulpes*.

Effective wildlife management requires knowledge of species' long-term population trends (Williams et al. 2002, White et al. 2015) to assist with harvest regulations and population management; however, these data can be logistically challenging to acquire and interpret because harvest-management efforts often occur across large spatiotemporal scales (White et al. 2015). Carnivores present additional challenges to monitoring because their cryptic behavior and low population densities often make them difficult to observe (Gese 2001, Allen et al. 2018). Harvest records are often interpreted as important indices of population size with which to assess long-term dynamic trends in species abundance (Viljugrein et al. 2001, Roberts and Crimmins 2010, Newsome and Ripple 2015, Ahlers and Heske 2017). For example, Newsome and Ripple (2015) examined fur return data and reported that fur returns for red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*) were related to gray wolf (*Canis lupus*) presence and potentially influenced by trophic interactions among these sympatric canids. But variation in trapper harvest data may be affected by factors independent of abundance (McKelvey et al. 2011, Kapfer and Potts 2012, Ahlers et al. 2016, Allen et al. 2019). Thus, it is important to evaluate sources of variation within trapper harvest data as a first step to better understanding changes in annual species-specific trapper harvest.

Trapper harvest data are products of numerous complex components. Trends in harvest data are influenced by

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species abundance (Allen et al. 2019) and the numbers and effort of individual trappers (Ruette et al. 2003, DeVink et al. 2011, Ahlers et al. 2016), which in turn are influenced by a suite of other factors. For example, pelt prices may influence harvest data (Elsken-Lacy et al. 1999, Roberts and Crimmins 2010, Ahlers et al. 2016), although this pattern is not universal across taxa or studies (Webb and Boyce 2009, Landriault et al. 2012). Furthermore, declining pelt prices are related to declines in trapper numbers across North America in recent decades (Siemer et al. 1994, Armstrong and Rossi 2000, McKelvey et al. 2011), which could result in harvest declines that are independent of changes in abundance.

Approximating population trends over time using harvest data is often dependent upon controlling for the numerous complex components that may influence harvest. Previous studies evaluating spatiotemporal variation in trapper harvest data collected since the 1970s have generally controlled for variation in trapper effort using number of trappers (Hiller et al. 2011, Suffice et al. 2020), pelt price as a proxy for trapper numbers (Gosselink et al. 2003, Ahlers and Heske 2017), or by using harvest per unit area or registered trapline (Webb and Boyce 2009, Robichaud and Boyce 2010). Previous researchers reported that gasoline prices and unemployment can influence harvest data by altering the economic costs and benefits of trapping (Stabler et al. 1990, Brinkman et al. 2014, Ahlers et al. 2016, Dorendorf et al. 2016). Winter weather conditions can also affect trapper harvest by reducing the effort of individual trappers or influencing animal behavior so as to alter their susceptibility to harvest (e.g., decreased activity in severe weather; Kapfer and Potts 2012, Landriault et al. 2012, Suffice et al. 2020). Consequently, it is important to investigate the effects of multiple components potentially influencing variation in harvest data.

Red foxes, gray foxes (*Urocyon cinereoargenteus*), and coyotes are largely sympatric canid species that are important predators in many ecosystems (Lindstrom et al. 1994, Sovada et al. 1995, Henke and Bryant 1999). These species occur in a variety of land cover types (Harrison 1997, Gehrt and Riley 2010, Soulsbury et al. 2010) and pose risks for human-wildlife conflict (Poessel et al. 2013). Furthermore, coyotes have expanded their distribution over the past century (Fener et al. 2005, Hody and Kays 2018) and their presence can directly (Farias et al. 2005, Gosselink et al. 2007) and indirectly (Fedriani et al. 2000, Linnell and Strand 2000, Gosselink et al. 2003) influence red fox and gray fox populations. All 3 species are harvested throughout North America (Siemer et al. 1994, Elsken-Lacy et al. 1999, Newsome and Ripple 2015) using similar trapping techniques (i.e., various sizes of concealed coil-spring foothold traps; Responsive Management 2015). Trapper harvest data therefore provide a potentially important data source with which to evaluate trends in these species.

We used long-term trapper harvest data (1976–2018) for red foxes, gray foxes, and coyotes from Illinois, USA, to determine how multiple factors reflecting socioeconomic and weather conditions influenced variation in trapper harvest data. First, we evaluated how pelt price, gasoline price, winter unemployment, and winter weather conditions influenced annual trapper harvest and *per capita* harvest (i.e., harvest per effective trapper or *per capita* harvest by trappers harvesting ≥1 individual of a given species). We also tested for trends (i.e., year effects) in annual trapper harvest and *per capita* harvest while controlling for the aforementioned factors. We predicted that the current and previous year's pelt prices would be positively related to canid (gray fox, red fox, and coyote) harvest through increased trapper numbers or effort in years with higher pelt prices (Roberts and Crimmins 2010, Ahlers et al. 2016). We also predicted that the number of trappers or individual trapper effort would be less in years with higher gas prices and more in years with higher winter unemployment (Stabler et al. 1990, Brinkman et al. 2014, Ahlers et al. 2016). Finally, we predicted negative effects of cold temperatures and high snowfall on canid harvest.

STUDY AREA

We used species-specific trapper harvest data collected across Illinois during 1976–2018. Illinois is characterized by low to moderate topographic relief (elevation ranged from 85–380 m above sea level) with the Chicago metropolitan area in the northeast, intensive row-crop agriculture of corn and soybeans in the northwest and central portions, and rolling, forested hills in the south. Approximately 75% of Illinois (~11 million ha) was devoted to agriculture, primarily in the central and northern portions of the state (U.S. Department of Agriculture 2017). Forest communities included multiple north-temperate hardwood species including oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), ash (*Fraxinus* spp.), American beech (*Fagus grandifolia*), and elm (*Ulmus* spp.; Bretthauer and Edgington 2002). Widespread terrestrial mammalian fauna in our study area included white-tailed deer (*Odocoileus virginanus*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), striped skunk (*Mephitis mephitis*), woodchuck (*Marmota monax*), squirrel (*Sciurus* spp.), and eastern cottontail (*Sylvilagus floridanus*). Statewide mean monthly temperature ranged from −4 to −1°C December–February, 5–11°C March–April, 17–24°C May–September, and 6–12°C October–November and mean monthly precipitation ranged from 5–7 cm December–February, 8–10 cm March–April, 8–11 cm May–September, and 8 cm October–November (https://mrcc.illinois.edu/CLIMATE/, accessed 10 Apr 2020).

The canid trapping seasons during our study were split between approximately the northern and southern halves of the state, with different season lengths in each. The northern half was open for an average of 59 days (mean opening date of 16 Nov, mean closing date of 12 Jan) and the southern half was open for an average of 61 days (mean opening date of 17 Nov, mean closing date of 16 Jan). The season length increased over the course of the study from 30 days during 1977–1983 to 77 days during 2005–2016 and 98 days during 2017–2018. There were no harvest limits for any of the 3 species during our study and harvest regulations remained relatively constant.

METHODS

Harvest Data and Covariates

We collected trapper harvest data using annual questionnaires delivered by mail. In 1976, we provided questionnaires to all licensed trappers ($n = 17{,}800$) and 3,119 were returned (17.5%). Beginning in 1977, we distributed questionnaires by mail to a random sample of license holders (Williams et al. 2018). Mean number of usable responses from 1977–2018 was 791 ± 171 (SD; range = 508–1,077) with a mean response rate of $74.7 \pm 7.2\%$ (range = 59.9–85.2%), which represented a mean of $15.7 \pm 7.6\%$ of licensed trappers (range = 4.9–33.0%). We did not consider non-response bias because of our high response rates. Total usable responses and response rate decreased during 1977–2018 ($r = -0.58$, $P < 0.001$ and $r = -0.84$, $P < 0.001$, respectively), whereas the proportion of license holders sampled tended to increase during this time ($r = 0.31$, $P = 0.044$). From each annual report, we extracted annual statewide estimates of trapper harvest, number of effective trappers, and *per capita* harvest (i.e., harvest per effective trapper) for each species. All surveys were conducted with approval from the University of Illinois Institutional Review Board (IRB 10236).

We measured covariates that we hypothesized *a priori* would cause variation in annual trapper harvest and *per capita* harvest (Table 1). We obtained the mean annual pelt price (U.S.$) of each species from publicly available annual Illinois Department of Natural Resources (IDNR) Fur Harvest Surveys (McTaggart 2018). We adjusted all pelt prices to 2018 prices to control for inflation using the mean annual seasonally adjusted Consumer Price Index (www.bls.gov/data/, accessed 4 Feb 2019). We obtained the mean annual retail gasoline prices (U.S.$/gallon nominal prices; www.eia.gov/outlooks/steo/realprices/, accessed 4 Feb 2019) and adjusted them to 2018 prices. We calculated the mean seasonally adjusted unemployment rate for Illinois during the trapping season (Nov–Jan; www.bls.gov/data/, accessed 30 Mar 2020).

We collected daily maximum air temperature (°C) and snow depth (cm) from National Oceanic and Aeronautics Administration (NOAA) weather stations ($n = 105$–162 stations/year) throughout Illinois during 1976–2018 using the RNOAA package (Chamberlain 2019) in Program R (version 3.5.0; R Core Team 2019). We made species-specific cutoffs by empirically modeling trapper harvest and *per capita* harvest as a function of weather covariates across a range of possible cutoffs (−30–15°C at increments of 5°C for temperature and 0–60 cm at 5-cm increments for snow). We retained the species-specific cutoff value with the greatest empirical support (see Statistical Analyses and Tables S1–S6, available online in Supporting Information). We defined an index of trapping season temperature severity as the mean proportion of days during the canid trapping season (i.e., 2 weeks prior to the earliest start date through latest end date following Kapfer and Potts [2012]) across stations where daily maximum air temperature (°C) was <20°C (red fox, gray fox, and coyote trapper harvest), 10°C (coyote *per capita* harvest), 0°C (red fox *per capita* harvest), or −5°C (gray fox *per capita* harvest; Table 1). We defined trapping season snow depth during each season for each species as the mean proportion of days during the

Table 1. Descriptions and summary statistics for covariates used in the analyses of annual trapper harvest (TRAP) and *per capita* harvest (PCH) for red fox, gray fox, and coyote in Illinois, USA, 1977–2018. Values for gray fox exclude covariate values from 2003 and 2015 which were excluded from analysis. All currency values are inflation-adjusted to 2018 values (U.S.$). The index of trapping season temperature severity (°C) and snow depth (cm) values are the species-specific cutoffs used to calculate their respective covariates.

Name	Description	$\bar{x}$	SD	Range
Year	Year of the study	1998	12	1977–2018
Current year's pelt price	Average pelt price in Illinois for the current year (t) adjusted to 2018 prices	red fox: $42.82 gray fox: $36.04 coyote: $23.85	red fox: $53.06 gray fox: $39.96 coyote: $23.09	red fox: $7.44–$236.71 gray fox: $6.63–$165.32 coyote: $6.18–120.67
Previous year's pelt price	Average pelt price in Illinois for previous year ($t - 1$) adjusted to 2018 prices	red fox: $47.43 gray fox: $38.75 coyote: $25.11	red fox: $58.09 gray fox: $42.04 coyote: $24.18	red fox: $9.00–$236.71 gray fox: $6.63–$165.32 coyote: $6.18–120.67
Gas price	Mean annual retail gasoline prices ($/liters, 2018 prices)	$9.91	$2.73	$6.01–$15.03
Unemployment	Mean seasonally adjusted unemployment rate in Illinois during the trapping season (Nov–Jan)	6.88	2.04	4.27–12.97
Index of trapping season temperature severity	Mean proportion of days during the trapping season where daily maximum air temperature was ≤ a species-specific cutoff	red fox, gray fox, and coyote TRAP (20°C): 0.94 red fox PCH (0°C): 0.19 gray fox PCH (−5°C): 0.08 coyote PCH (10°C): 0.65	red fox, gray fox, and coyote TRAP (20°C): 0.04 red fox PCH (0°C): 0.07 gray fox PCH (−5°C): 0.05 coyote PCH (10°C): 0.09	red fox, gray fox, and coyote TRAP: 0.83–1.00 red fox PCH: 0.08–0.36 gray fox PCH: 0.01–0.20 coyote PCH: 0.48–0.82
Trapping season snow depth	Mean proportion of days during the trapping season where daily snow depth was ≥ a species-specific cutoff	red fox (0 cm): 0.18 gray fox (0 cm): 0.18 coyote (0 cm): 0.18	red fox (0 cm): 0.12 gray fox (0 cm): 0.12 coyote (0 cm): 0.12	red fox: 0.01–0.50 gray fox: 0.01–0.50 coyote: 0.01–0.50

canid trapping season where mean daily snow depth (cm) across stations was >0 cm (Table 1).

Statistical Analyses

We used Spearman's rank correlations to test for associations between trapper harvest and 3 variables, the number of effective trappers, the current year's pelt prices, and the previous year's pelt prices, for each species. We conducted all analyses in R.

We developed 12 *a priori* candidate models describing hypothesized relationships between trapper harvest and *per capita* harvest and our covariates (Tables S7–S8, available online in Supporting Information); however, current and previous year's pelt price and year were included in separate models because of collinearity ($r = -0.52$ to -0.71). When collinearity between the index of trapping season temperature severity and snow depth was >0.60, we retained the covariate with greatest empirical support (Table S7–S8, see Results). Collinearity among covariates within candidate models was low ($|r| \leq 0.52$) and variance inflation factors were ≤1.59. Gray fox *per capita* harvest in 2003 (5.43) was an outlier with respect to all other years (range = 0.00–3.07). We therefore excluded 2003 and 2015 (when no gray foxes were harvested) from the analysis. We evaluated the degree of temporal residual autocorrelation using the acf function in R (Zuur et al. 2009).

We modeled log-transformed trapper harvest using generalized linear models (GLM) with Gaussian error distributions. Models for trapper harvest all showed significant residual autocorrelation at the first lag (i.e., 1 yr). Although this generally does not bias coefficient estimates of linear models, it will underestimate the standard errors resulting in inflated Type I errors. Modeling residual autocorrelation requires additional model parameters and may substantially change the coefficient estimates, making it difficult to interpret the estimated effects (Fieberg and Ditmer 2012). We therefore used a resampling approach to minimize the effects of residual autocorrelation at the 1-year lag while maintaining our original model parameterizations wherein we randomly sampled half of our data without replacement ($n = 21$ of 42) and fit models using the subsampled dataset, repeating this process 10,000 times (De Bin et al. 2016). We used the remaining 21 hold-out observations as training data to evaluate the predictive ability of each model using Lin's (1989) concordance correlation coefficient (CCC), which ranges from 0–1 and quantifies the deviation from a line with intercept = 0 and slope = 1 between the observed and predicted values.

We calculated the mean rank and median difference in Akaike's Information Criterion adjusted for small sample sizes (ΔAIC_c; Burnham and Anderson 2002), R^2, and CCC values for each model across all subsamples. We calculated the proportion of times a model was the top-ranked model (π) as an analog to AIC_c model weight (Burnham and Anderson 2002) and drew inferences from models with cumulative π exceeding 0.95 (i.e., 95% confidence set; Anderson 2008). For each random subsample, we calculated the model-averaged coefficient (β) estimates across all models containing a given covariate (Grueber et al. 2011) and standardized covariates by their partial standard deviation (Cade 2015) using the MuMIn package (Barton 2019). We also calculated model-averaged predicted values for each covariate across all models while holding all other covariates constant at their means. We report the median model-averaged coefficient estimates and predicted values and interpret their 2.5th and 97.5th quantiles as 95% confidence intervals.

Because collinearity prevented us from jointly modeling the effects of year and pelt price on trapper harvest, we conducted an additional analysis to test for trends in trapper harvest while controlling for pelt price. We divided trapper harvest by the current or previous year's pelt price (Ahlers and Heske 2017) and modeled the log-transformed adjusted trapper harvest as a function of year. We then re-ran our subsampling analysis using 10,000 random subsamples and report the median and 95% confidence intervals of the coefficient estimate for year.

We modeled *per capita* harvest using GLM with gamma error distributions and log links to accommodate our right-skewed positive-only data. Models for *per capita* harvest did not show consistent significant residual autocorrelation. We ranked models using AIC_c and drew inferences from models with cumulative AIC_c weights (w_i) exceeding 0.95 (i.e., 95% confidence set; Anderson 2008). We report the proportion of deviance (D^2) explained by each candidate model. We report model-averaged coefficient estimates and 95% confidence intervals across models within the 95% confidence set as described above using the MuMIn package. We also report model-averaged predicted values for each covariate across the 95% confidence set. We conducted the same resampling analysis for *per capita* harvest to calculate the predictive performance of our candidate models for each species using the median CCC across 10,000 resampled data sets.

RESULTS

Trapper Harvest

We estimated that 143,024 red foxes, 54,100 gray foxes, and 253,857 coyotes were harvested in Illinois during 1976–2018. During this time, the number of trapping licenses sold declined from 1976 until the early 1990s, after which the number of trapping licenses sold increased to approximately a third of those of the 1970s (Appendix A). Harvest and number of effective trappers were more correlated for foxes (red fox: $r_s = 0.91$, $P < 0.001$; gray fox: $r_s = 0.96$, $P < 0.001$) than for coyote ($r_s = 0.53$, $P < 0.001$). Harvest was correlated with current and previous year's pelt prices for red fox (current year: $r_s = 0.83$, $P < 0.001$; previous year: $r_s = 0.78$, $P < 0.001$) and gray fox (current year: $r_s = 0.64$, $P < 0.001$; previous year: $r_s = 0.64$, $P < 0.001$) but not coyote (current year: $r_s = 0.21$, $P = 0.18$; previous year: $r_s = 0.20$, $P = 0.20$).

Both harvest and number of effective trappers for red fox and gray fox showed non-linear trends with strong declines until the early 1990s, after which both metrics remained low but relatively stable (Fig. 1). Median annual trapper harvest

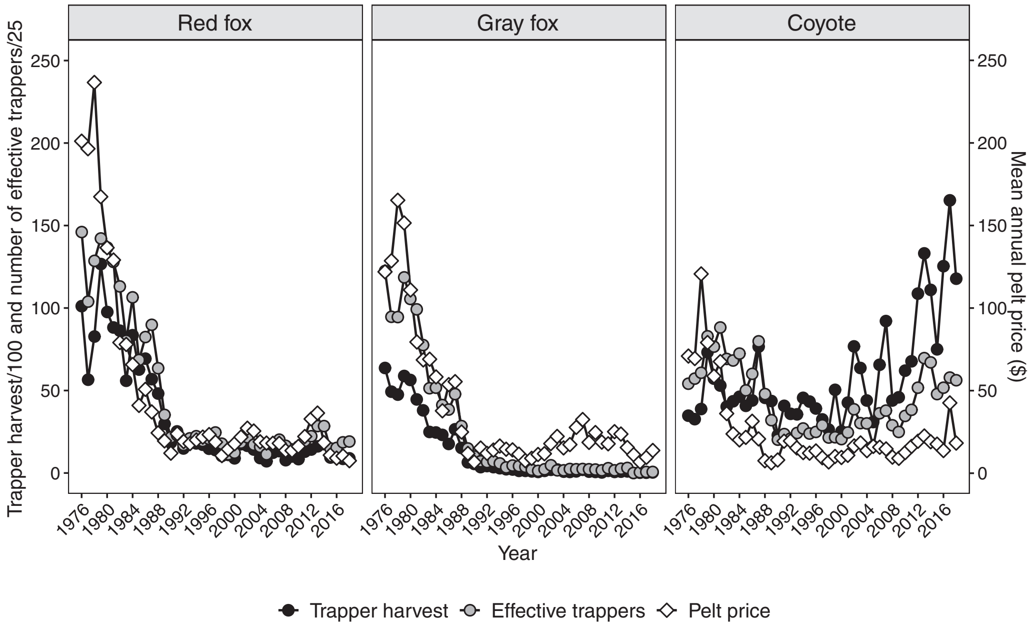

Figure 1. Estimated trapper harvest, number of effective trappers (i.e., trappers harvesting ≥1 individual of given species), and inflation-adjusted mean annual pelt price for red fox, gray fox, and coyote in Illinois, USA, 1976–2018. We divided trapper harvest by 100 and number of effective trappers by 25 for visualization.

during 1976–1989 for red fox and gray fox was 7,600 and 3,222, respectively, compared to 1,316 and 102 (with no recorded gray fox harvest in 2015) during 1990–2017, respectively (Table 2). In contrast, harvest and number of effective trappers for coyote increased beginning in the early 1990s (Fig. 1). Median annual trapper harvest for coyotes was 4,380 during 1976–1989 and 4,585 from 1990–2018 (Table 2).

Red fox.—The top model ($\pi = 0.60$) for red fox harvest contained year, gas price, and winter unemployment (median $R^2 = 0.82$; Table 3). The second-ranked model contained only year ($\pi = 0.18$, median $R^2 = 0.74$). Models with year had a cumulative π of 0.81 and greater empirical support compared to models with previous or current year's pelt prices (cumulative $\pi = 0.14$ and 0.05, respectively). Red fox harvest was negatively associated with year ($\beta = -0.73$, 95% CI = − 0.88 to −0.47; Figs. 2 and 3) and positively associated with gas price ($\beta = 0.13$, 95% CI = − 0.27–0.29) and winter unemployment ($\beta = 0.08$, 95% CI = − 0.04–0.34; Figs. 2 and 3), although the model-averaged effect sizes for these latter 2 covariates were lower. After dividing red fox trapper harvest by current or previous year's pelt price (Fig. 4), the 95% confidence interval of the coefficient estimate for year included zero (current year: $\beta = -0.08$, 95% CI = − 0.28–0.06; previous year: $\beta = -0.05$, 95% CI = − 0.22–0.07), indicating uncertain empirical support for a decline in price-adjusted red fox trapper harvest during our study.

Gray fox.—The top model ($\pi = 0.93$) for gray fox harvest contained year, gas price, and winter unemployment (median $R^2 = 0.94$; Table 3). Models that included year had a cumulative π of 0.99 and greater empirical support compared to models with previous or current year's pelt prices (cumulative $\pi = 0.01$ and 0.00, respectively). Gray fox harvest was negatively associated with year ($\beta = -1.57$, 95% CI = − 1.89 to −1.10; Figs. 2 and 3) and positively associated with gas price ($\beta = 0.30$, 95% CI = 0.07–0.44) and winter unemployment ($\beta = 0.05$, 95% CI = − 0.08–0.21; Figs. 2 and 3) though the model-averaged effect size for winter unemployment was relatively low. The 95% confidence interval of the coefficient estimate for the effect of year on gray fox trapper harvest divided by current or previous year's pelt price (Fig. 4) excluded zero (current year:

Table 2. Estimated annual trapper harvest, number of effective trappers (i.e., trappers harvesting ≥1 individual of given species), and *per capita* harvest for red fox, gray fox, and coyote in Illinois, USA, 1976–1989 and 1990–2018. We present the inter-quartile range (IQR) as the 25th and 75th quantiles.

		Trapper harvest			Number of effective trappers			*Per capita* harvest		
Species	**Dates**	**Median**	**IQR**	**Range**	**Median**	**IQR**	**Range**	**Median**	**IQR**	**Range**
Red fox	1976–1989	7,600	5,658–8,775	2,983–12,659	2,628	2,018–3,209	881–3,652	2.95	2.76–3.31	2.18–3.67
Gray fox	1976–1989	3,222	2,347–4,882	640–6,363	1,614	1,071–2,451	371–3,059	1.99	1.91–2.12	1.73–2.24
Coyote	1976–1989	4,380	4,035–5,124	3,266–7,649	1,610	1,372–1,891	798–2,205	2.75	2.55–3.46	2.28–5.48
Red fox	1990–2018	1,316	932–1,641	705–2,528	464	399–541	283–711	2.67	2.35–3.32	1.86–4.42
Gray fox	1990–2018	102	72–211	0–553	61	42–103	0–249	1.85	1.30–2.07	0.00–5.43
Coyote	1990–2018	4,585	3,903–7,678	2,298–16,525	724	596–965	406–1,741	7.07	6.25–7.95	4.49–11.41

Table 3. Candidate model rankings for factors influencing annual trapper harvest for red fox, gray fox, and coyote in Illinois, USA, 1977–2018. We calculated rankings by fitting candidate models to 21 randomly selected data points across 10,000 iterations. We present the number of model parameters (K), median difference in Akaike's Information Criterion adjusted for small sample sizes (ΔAIC_c), proportion of iterations a model was the top-ranked model (π), cumulative π (cum. π), and Lin's (1989) concordance correlation coefficient (CCC) between the observed and predicted values for the remaining 21 data points. We report models from the 95% confidence set and the null model. Variables include year, gas price (gas), unemployment (unemp), snow depth (snow), an index of trapping season temperature severity (temp), and previous year's pelt price ($pelt_{t-1}$).

Models	K	Mean rank	Median ΔAIC_c	π	Cum. π	Median R^2	Median CCC
Red fox							
Year + gas + unemp	5	1.72	0.00	0.60	0.60	0.82	0.91
Year	3	2.82	3.55	0.18	0.78	0.74	0.85
$Pelt_{t-1}$ + gas + unemp	5	4.41	8.04	0.09	0.88	0.74	0.86
Year + snow + temp	4	4.67	7.00	0.03	0.90	0.75	0.87
$Pelt_{t-1}$ + snow + temp	4	4.84	9.20	0.04	0.94	0.73	0.85
$Pelt_{t-1}$	3	5.84	11.17	0.01	0.95	0.64	0.78
Null	2	10.70	30.93	0.00	1.00	0.00	0.00
Gray fox							
Year + gas + unemp	5	1.08	0.00	0.93	0.93	0.94	0.97
Null	2	10.58	49.57	0.00	1.00	0.00	0.00
Coyote							
Year	3	1.61	0.00	0.66	0.66	0.30	0.49
Year + gas + unemp	5	3.00	2.50	0.22	0.89	0.38	0.61
Year + snow	4	3.48	2.96	0.02	0.90	0.28	0.50
Gas + unemp	4	4.94	6.11	0.05	0.95	0.17	0.38
Null	2	5.32	6.62	0.02	0.97	0.00	0.00

$\beta = -1.05$, 95% CI $= -1.23$ to -0.91; previous year: $\beta = -0.99$, 95% CI $= -1.15$ to -0.87), indicating a decline in price-adjusted gray fox trapper harvest during our study.

Coyote.—The top-ranked model ($\pi = 0.66$) for coyote harvest contained only year (Median $R^2 = 0.30$), and the second-ranked model ($\pi = 0.22$) included year, gas price, and winter unemployment (median $R^2 = 0.38$; Table 3). Models that included year had a cumulative π of 0.90 and greater empirical support compared to models with previous or current year's pelt prices (cumulative $\pi = 0.01$ and 0.02, respectively). Coyote trapper harvest was positively associated with year ($\beta = 0.25$, 95% CI $= 0.11$–0.37; Figs. 2 and 3) and gas price although model-averaged coefficient estimate for gas price was lower ($\beta = 0.16$, 95% CI $= 0.02$–0.28;

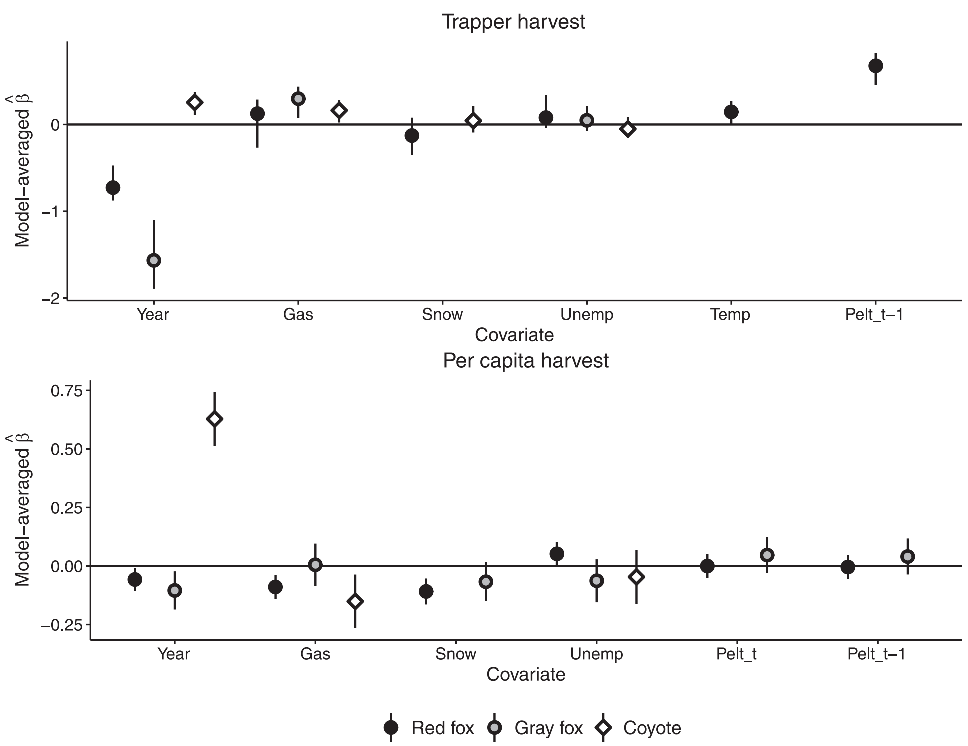

Figure 2. Model-averaged standardized coefficient estimates and 95% confidence intervals (CI) for covariates influencing annual trapper harvest (log-transformed) and *per capita* harvest for red fox, gray fox, and coyote in Illinois, USA, 1977–2018. We standardized coefficients using the partial standard deviations of their respective covariate and averaged them across all models containing a given covariate within the 95% confidence set. Variables include gas price (gas), unemployment (unemp), snow depth (snow), an index of trapping season temperature severity (temp), and current and previous year's pelt price ($pelt_t$ and $pelt_{t-1}$).

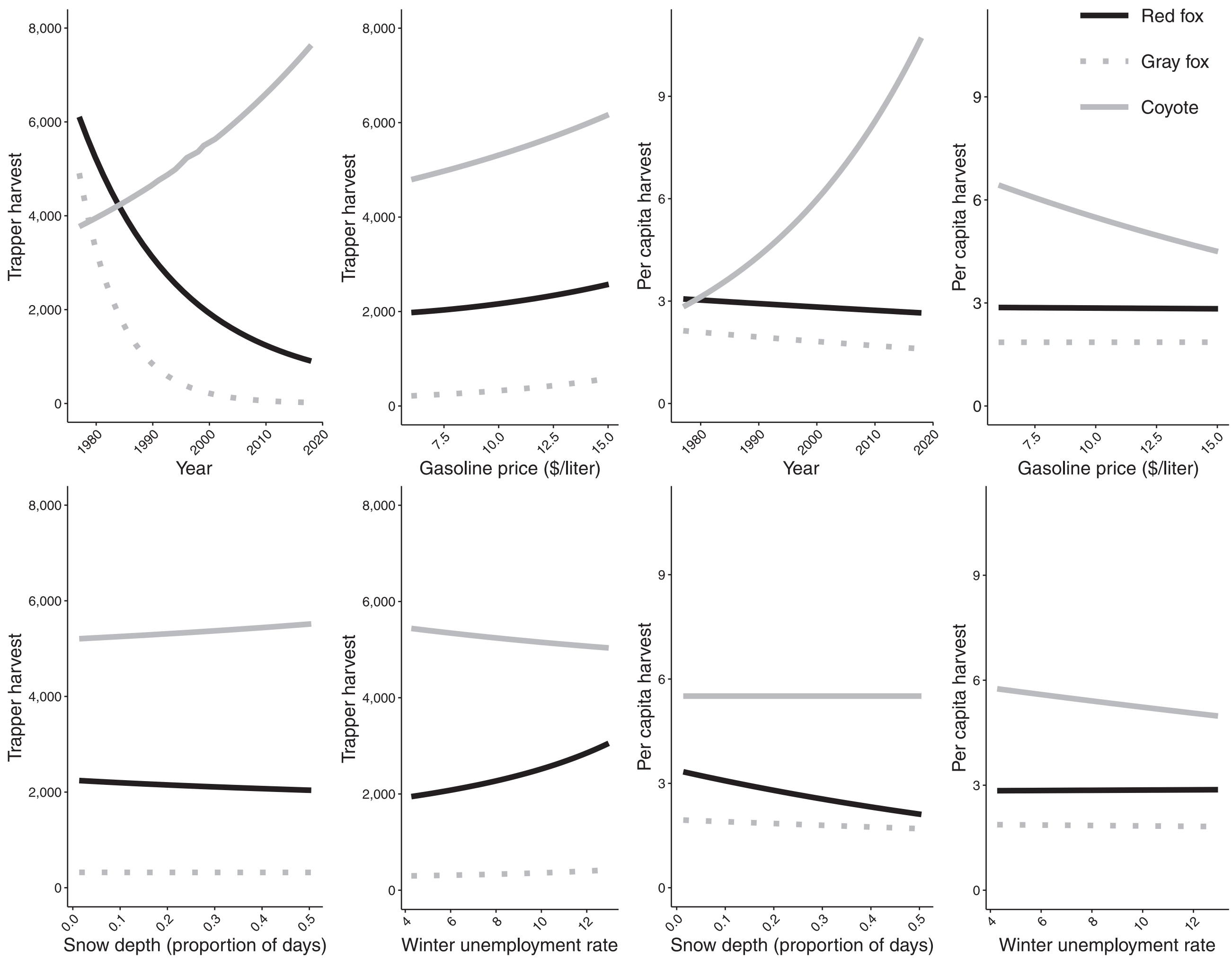

Figure 3. Model-averaged predicted values for annual trapper harvest and *per capita* harvest for red fox, gray fox, and coyote in Illinois, USA, 1977–2018 as a function of select covariates across all models in the 95% confidence set. For a given covariate, we held all other covariates constant at their mean value. Variables include gas price (gas), unemployment (unemp), and snow depth (snow).

Figs. 2 and 3). The 95% confidence interval of the coefficient estimate for the effect of year on coyote harvest divided by current or previous year's pelt price (Fig. 4) excluded zero (current year: $\beta = 0.57$, 95% CI = 0.36–0.73; previous year: $\beta = 0.63$, 95% CI = 0.43–0.79), indicating an increase in price-adjusted coyote trapper harvest during our study.

Per Capita Harvest

Median annual *per capita* harvest was 2.80 (inter-quartile range [25th and 75th quantiles; IQR] = 2.49–3.35) for red fox, 1.98 (IQR = 1.55–2.11) for gray fox, and 6.25 (IQR = 3.68–7.32) for coyotes (Table 2). *Per capita* harvest was relatively stable over time for red foxes and gray foxes but increased for coyotes (Fig. 4).

Red fox.—The top model ($w_i = 0.66$, $D^2 = 0.45$; Table 4) for red fox *per capita* harvest contained year and snow depth during the trapping season (using the 0-cm cutoff; Table S4). The second-best model contained only snow depth ($w_i = 0.18$, $D^2 = 0.38$), whereas the third-best model contained snow depth and the previous year's pelt price ($w_i = 0.05$, $D^2 = 0.38$). Models including year had a cumulative w_i of 0.70 and greater empirical support than compared to models with current or previous year's pelt prices (cumulative w_i both = 0.06). Red fox *per capita* harvest was negatively related with year ($\beta = -0.06$, 95% CI = − 0.11 to −0.01) and snow depth ($\beta = -0.11$, 95% CI = − 0.17 to −0.06; Figs. 2 and 3).

Gray fox.—The top model ($w_i = 0.36$, $D^2 = 0.18$; Table 4) for gray fox *per capita* harvest contained only year ($\beta = -0.10$, 95% CI = − 0.19 to −0.02). The second-best model had similar support ($w_i = 0.32$, $D^2 = 0.22$) and contained year and snow depth (using the 0-cm cutoff; Table S5), whereas the third-best model contained year, gas price, and winter unemployment ($w_i = 0.11$, $D^2 = 0.23$). Models that included year had a cumulative w_i of 0.79, providing more empirical support than models with current or previous year's pelt prices (cumulative $w_i = 0.06$ and 0.05, respectively). The negative model-averaged coefficient estimate of year indicated declines in gray fox *per capita* harvest over time (Figs. 2 and 3).

Coyote.—The top model ($w_i = 0.93$, $D^2 = 0.77$) for coyote *per capita* harvest contained year, gas price, and

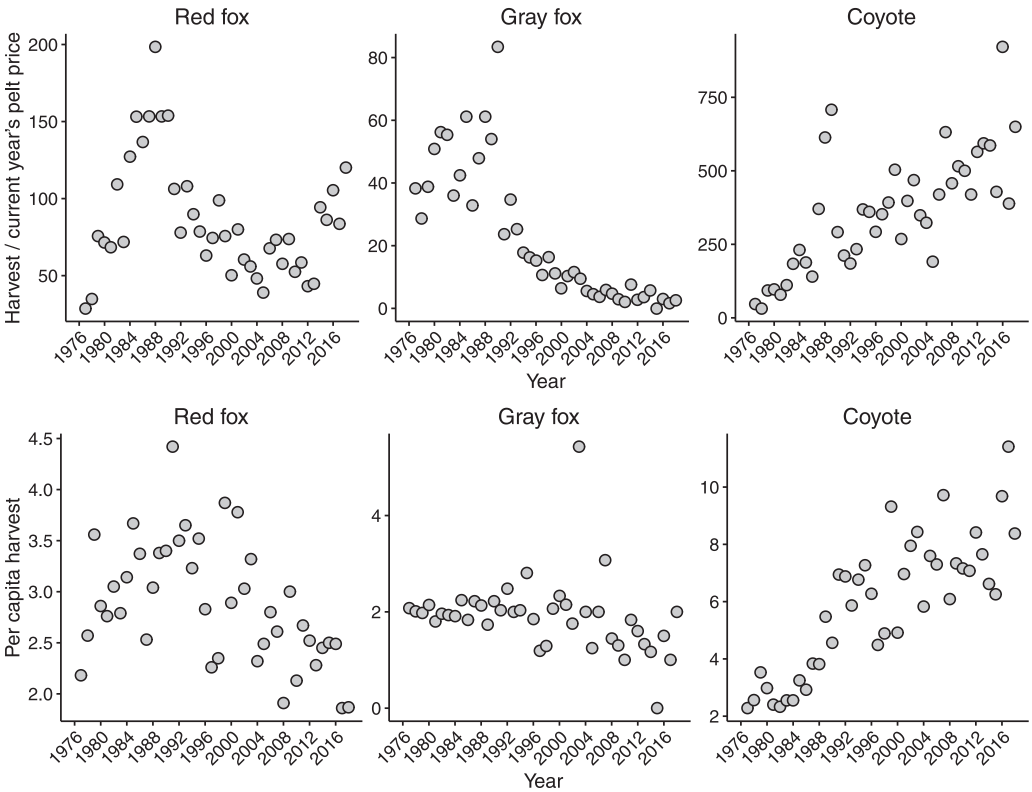

Figure 4. Annual trapper harvest divided by the current year's inflation-adjusted mean annual pelt price and *per capita* harvest (i.e., trappers harvesting ≥1 individual of a given species) for red fox, gray fox, and coyote in Illinois, USA, 1977–2018.

unemployment (Table 4). Coyote *per capita* harvest was positively associated with year ($\beta = 0.63$, 95% CI = 0.51–0.74) and negatively related to gas price ($\beta = -0.15$, 95% CI = − 0.27 to −0.04) and unemployment ($\beta = -0.05$, 95% CI = − 0.16–0.07; Figs. 2 and 3).

DISCUSSION

We simultaneously assessed the influence of multiple economic and environmental factors on annual harvest reports of 3 sympatric canid species across large spatiotemporal scales. Additionally, our study highlights the importance of incorporating specific economic information into models used to infer species-specific population trends. For example, including gas price and winter unemployment rate with year in models for annual trapper harvest of red foxes and gray foxes substantially improved the degree of model support relative to models using only year. In contrast to the fox species, the model with only year strongly outperformed

Table 4. Candidate model rankings based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for factors influencing annual *per capita* harvest for red fox, gray fox, and coyote in Illinois, USA, 1977–2018. We report models from the 95% confidence set and the null model. We present the number of parameters (K), log-likelihood (LL), difference in AIC_c (ΔAIC_c), model weight (w_i), cumulative model weight (cum. w_i), proportion of deviance explained (D^2), and median Lin's (1989) concordance correlation coefficient (CCC) between the observed and predicted values across 10,000 resampled data sets. Variables include year, gas price (gas), unemployment (unemp), snow depth (snow), and current and previous year's pelt price ($pelt_t$ and $pelt_{t-1}$).

Models	K	LL	ΔAIC_c	w_i	Cum. w_i	D^2	Median CCC
Red fox							
Snow + year	4	−23.79	0.00	0.66	0.66	0.45	0.60
Snow	3	−26.31	2.59	0.18	0.84	0.38	0.54
Snow + $pelt_{t-1}$	4	−26.30	5.02	0.05	0.89	0.38	0.54
Snow + $pelt_t$	4	−26.31	5.04	0.05	0.95	0.38	0.54
Null	2	−36.49	20.63	0.00	1.00	0.00	0.00
Gray fox							
Year	3	−21.11	0.00	0.36	0.36	0.18	0.30
Snow + year	4	−20.00	0.27	0.32	0.68	0.22	0.35
Gas + unemp + year	5	−19.78	2.45	0.11	0.79	0.23	0.37
Snow	3	−22.73	3.25	0.07	0.86	0.11	0.20
Snow + $pelt_t$	4	−21.94	4.14	0.05	0.90	0.14	0.25
Snow + $pelt_{t-1}$	4	−22.13	4.53	0.04	0.94	0.14	0.24
Null	2	−25.07	5.59	0.02	0.96	0.00	0.00
Coyote							
Gas + unemp + year	5	−64.09	0.00	0.93	0.93	0.77	0.83
Null	2	−95.59	55.63	0.00	1.00	0.00	0.00

all other candidate models when investigating annual coyote trapper harvest, suggesting less of an effect of economic and environmental factors. Gas price and employment status can affect trappers' decisions to engage in trapping and the effort they expend (Stabler et al. 1990, Brinkman et al. 2014, Dorendorf et al. 2016). After controlling for these factors, we still observed strong negative trends for red foxes and gray foxes and strong positive trends for coyotes, respectively, in annual trapper harvest. This information is important to managers interested in long-term population dynamics of canids, particularly with recent efforts to understand gray fox population declines in prairies (Illinois Department of Natural Resources 2005, Cooper et al. 2012). Additionally, this information is relevant to researchers using long-term canid harvest data to infer trophic effects (Newsome and Ripple 2015) and human disease risks (Levi et al. 2012).

Annual trapper harvest was strongly correlated with the number of effective trappers for red foxes and gray foxes but was moderately correlated for coyotes. The importance of controlling for variation in individual trapper effort when using trapper harvest data is widely recognized (Gese 2001, Ruette et al. 2003, Landriault et al. 2012), although data on individual trapper effort were unavailable in our study. But when controlling for trapper numbers, both using annual trapper harvest divided by pelt price as a proxy for trapper numbers and *per capita* harvest, we still found increasing trends for coyotes. In contrast, trends for gray fox and red fox after controlling for trapper numbers were much weaker but still negative. This may suggest that declines in red fox and gray fox annual trapper harvest are influenced in part by declining trapper numbers in response to declining pelt prices (Ahlers et al. 2016). Our results therefore reinforce the recommendation to control for variation in trapper numbers and effort when drawing inferences from trapper harvest data.

Other economic and environmental factors had species-specific influences on variation in *per capita* harvest. The negative relationship between red fox and, to a lesser extent, gray fox *per capita* harvest and snow depth could reflect reduced trapper effort (Stabler et al. 1990) and reduced susceptibility of each species to trapping during years of high snowfall (Kapfer and Potts 2012, Suffice et al. 2020). In contrast, coyote *per capita* harvest was negatively related to gas price. Trappers may limit their time trapping and the spatial extent of their trapping in response to higher gas prices (Brinkman et al. 2014, Ahlers et al. 2016). Unemployment had a negative, but weaker, relationship with *per capita* coyote harvest contrasting with positive relationships between unemployment and number of trappers found by other studies (Stabler et al. 1990, Ahlers et al. 2016). The financial costs of trapping (e.g., price of trapping supplies and gas, time lost from other income-producing activities) may preclude trappers from participating during periods of relatively high unemployment, although we lacked data to test that hypothesis.

Factors other than those we considered may also influence variation in *per capita* harvest, particularly for red foxes and gray foxes given the relatively low explanatory power of our models. Trapper success may vary spatially depending on local habitat conditions and land access (Miller and Vaske 2003) and according to trapper skill, experience, or motivation (Ruette et al. 2003, Zwick et al. 2006). Additionally, differences in species ecology (e.g., home range size) or the social value of species (e.g., coyotes perceived as predators) may influence species-specific trapping effort and success. Changes in trap types within and among species over time may influence variation in trapper success. For example, although approximately a third of Midwest trappers used #1 1/2 coil-spring traps for red foxes, gray foxes, and raccoons during 2014–2015 (Responsive Management 2015), a greater proportion of raccoon trappers may have used coil-spring traps early in our study before the availability of dog-proof raccoon traps and therefore taken foxes incidentally. But we suspect that this putative shift is not sufficient to account for dramatic declines in red fox and gray fox annual trapper harvest. This difficulty in prediction highlights the importance of collecting data on individual and species-specific trapper effort and success to fully understand variation in trapper harvest data.

The challenges in inferring mechanisms responsible for trends in trapper harvest data are highlighted with red foxes in Illinois. The steep decline in red fox harvest during the 1970s and 1980s coincided with a similar decline in pelt price and number of trapping licenses sold, likely because of declining trapper participation in response to declining pelt prices (Stabler et al. 1990, Siemer et al. 1994, Ahlers et al. 2016). Evaluating red fox *per capita* harvest partially controls for changes in trapper numbers, and after we controlled for other factors, we again found evidence, albeit weaker, of decline. Declines in these indices may not indicate declines in red fox abundance but instead shifts in availability due to increased use of urban areas (Gosselink et al. 2003). Red foxes are urban adapters (Soulsbury et al. 2010, Mueller et al. 2018) and broad-scale distribution shifts to urban areas may reduce red fox availability to trappers. Berry et al. (2017) did not find evidence of red fox in rural grasslands in central Illinois over 2 years of distribution surveys. Our random sample of licensed trappers did not account for the spatial distribution of trappers or land cover types used by trappers and may introduce bias if red foxes have shifted to urban areas, especially if they are not harvested. The contrasting inferences amongst our different harvest-based indices suggests a limited ability to detect trends in red fox abundance from trapper harvest data.

The magnitude of gray fox harvest declines also weakened after controlling for changes in trapper numbers but not to the same extent as with red foxes. In fact, none of the trapper respondents in 2015 reported harvesting a gray fox. Gray fox trapper harvest, both with and without adjusting for pelt price, and gray fox *per capita* harvest consistently declined, even after 1990 when gray fox pelt prices and trapping license sales increased. In Illinois, gray foxes are considered a species in greatest need of conservation (Illinois Department of Natural Resources 2005), and gray fox site extinction rates were greater than site colonization rates in southern Illinois (Lesmeister et al. 2015). Therefore, although declines in harvest-based indices for gray fox could be an artifact of our trapper survey methods (e.g., random statewide sampling), these declines are consistent with hypothesized declines in gray fox abundances in the midwestern United States (Cooper et al. 2012, Lesmeister et al. 2015, Rich et al. 2018).

We observed strong concordance among indices for coyotes, showing consistent increases with and without controlling for potential confounding factors. Although we did find that socioeconomic factors affected annual trapper harvest and *per capita* harvest, these effects did not obscure the overall increasing trend. Our results are consistent with the expansion of this species into the eastern United States in past decades (Fener et al. 2005, Hody and Kays 2018) and the widespread occurrence of coyotes throughout the Midwest. Lesmeister et al. (2015) reported coyotes to be nearly ubiquitous in southern Illinois, as did Rich et al. (2018) in southern Ohio, USA. But increased coyote harvest could also reflect changes in trapper focus and behavior. The number of trappers primarily targeting coyotes increased from 27% in 1992 to 55% in 2015 (Responsive Management 2015). Increased *per capita* coyote harvest could also reflect increased effort of coyote trappers for the purposes of predator control (Glas et al. 2019), contemporary interest in predator trapping, or as a response to increased season length, but additional data are needed to test these hypotheses.

Trends in annual canid harvest may be similar across geopolitical boundaries. To fully understand dynamics in these trends, managers should jointly assess species-specific harvest across state and province jurisdictions. To do this, managers should work in concert to develop similar data collection strategies to make annual harvest comparable across large spatiotemporal scales. Currently, states and provinces have dissimilar trapping regulations and methods to estimate annual trapper harvest. By working concurrently to sample trapper effort and success, regardless of dissimilar trapping regulations, future investigations into canid harvest trends can assess factors influencing large-scale changes in harvest. We recommend that state and provincial furbearer biologists work together to develop standardized fur trapper sampling regimes to build a more complete annual trapper harvest dataset. Further, it is imperative that state agencies employ detailed quantitative survey instruments designed to measure harvest, trapper methods, effort, and activities (e.g., targeted species) to maximize data comparability across regional and national scales to enable species population modeling at various scales. We also recommend that, where resources permit, wildlife managers collect fine-scale harvest data (e.g., county-level) and additional data on trapper effort (e.g., species- or trap-specific number of trap nights) to increase the utility of harvest data for evaluating population trends.

MANAGEMENT IMPLICATIONS

Trapper harvest data have the potential to provide valuable information for wildlife managers only if they recognize and account for the factors that influence annual fur harvest reports. We suggest a careful examination of all available information related to trapper harvest data before drawing inferences regarding trends in trapper harvest or population abundance. In particular, managers should use caution when inferring trends from annual harvest numbers without accounting for trapper numbers. The effects of socio-economic factors and weather conditions may differ across species and managers should evaluate the effects of these factors separately across species. Maintaining standardized databases of these potentially confounding factors, including number of trappers targeting a given species, inflation-adjusted pelt and gasoline prices, and winter weather data, alongside harvest data can facilitate future analyses across species. For instance, this information would be useful to include in the Association of Fish and Wildlife Agencies (AFWA) United States Furbearer Harvest Statistics Database (https://www.fishwildlife.org/afwa-inspires/furbearer-management, accessed 13 Apr 2020). Finally, evidence of declining red fox and gray fox harvest trends highlights the need for additional research to evaluate the extent of these declines and their mechanistic causes.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

APPENDIX A. TRAPPING LICENSES

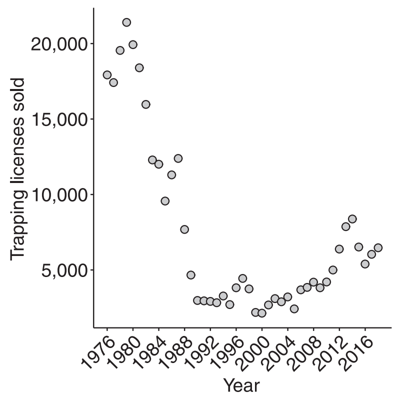

Figure A1. Number of trapping licenses sold in Illinois, USA, 1976–2018.