



Long-term data reveal equivocal evidence for intraguild suppression among sympatric canids

Javan M. Bauder¹ · Maximilian L. Allen¹ · Adam A. Ahlers² · Thomas J. Benson¹ · Craig A. Miller¹ · Kirk W. Stodola¹

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Abstract

Interspecific interactions among predators can shape ecological communities across trophic levels, including among predator guilds. The strength and directions of these interactions, however, may vary spatially and temporally in regions undergoing widespread landscape changes (e.g., urbanization, agricultural production). We investigated intraguild effects of coyotes (*Canis latrans*), a de facto apex predator, and land-cover changes on abundance indices of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) using two long-term and independent time series: direct observations of canids by archery deer hunters (26 years) and harvest data from canid trappers (41 years) from across Illinois, USA. Abundance indices from both time series for red and gray foxes declined whereas coyote abundance indices increased, suggesting increasing coyote abundance may have led to decreases in fox population abundances. Empirical support among candidate models explaining fox declines was generally equivocal yet differed between fox species. Models including effects of coyote abundance were generally competitive for red foxes and estimated negative coyote effects even after controlling for declining farm size. The empirical support among our landscape hypotheses also varied by species despite increasing forest cover and farm size during our study. The estimated effects of coyote in our study were weaker than reported at more northerly latitudes suggesting that increasing coyote populations may not be fully responsible for observed declines in fox populations in the midwestern USA.

Keywords Carnivore community · Competition · Interspecific competition · Landscape change · Population monitoring · Top-down effects

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✉ Javan M. Bauder
jbauder@arizona.edu

¹ Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, IL, USA

² Department of Horticulture and Natural Resources, Kansas State University, Manhattan, KS, USA

Introduction

Predators can elicit top-down effects on ecological communities, not only through effects on herbivores but also on sympatric predators (Estes and Palmisano 1974; McLaren and Peterson 1994; Ripple et al. 2014). Inter-predator effects may include direct interactions between species (Wootton 1994) such as intraguild predation (Palomares and Caro 1999; Prugh and Sivy 2020) or spatiotemporal avoidance of larger predators by smaller predators (Swanson et al. 2014; Wang et al. 2015; Shores et al. 2019). Such effects may also be indirect, modifying the behavior and/or abundance of another species (Wootton 1994). Among terrestrial mammalian predators, relatively large-bodied species (i.e., apex predators) may restrict the abundance or behavior of smaller-bodied species (i.e., mesopredators) (Prugh et al. 2009; Levi and Wilmers 2012) that in turn can produce cascading ecological effects (Beschta and Ripple 2009; Estes et al. 2011; Ripple et al. 2014). Alternatively, predator guilds may coexist at relatively broad spatial scales due to niche partitioning or fine-scale spatiotemporal avoidance (Steinmetz et al. 2013; Swanson et al. 2014; Sivy et al. 2017). Understanding population-level consequences of inter-specific predator interactions due to changing predator communities is, therefore, important not only from a basic ecological standpoint but also to inform species conservation efforts (Linnell and Strand 2000; DeCesare et al. 2010).

Coyotes (*Canis latrans*) often exhibit negative effects on smaller predators, including foxes (*Vulpes* and *Urocyon* spp). For example, coyotes are predators of all sympatric fox species (Sargeant and Allen 1989; Cypher and Spencer 1998; Fedriani et al. 2000; Kamler et al. 2003; Farias et al. 2005; Gosselink et al. 2007; Karki et al. 2007). Foxes may also avoid coyotes both temporally (Lesmeister et al. 2015; Wang et al. 2015; LeFlore et al. 2019) and spatially (Harrison et al. 1989; Gosselink et al. 2003; Chamberlain and Leopold 2005), and fox site occupancy and abundance may be negatively associated with coyote presence and abundance across multiple spatial scales (Fedriani et al. 2000; Robinson et al. 2014; Egan et al. 2021; Schooley et al. 2021). Past studies demonstrate that red fox abundance was negatively associated with coyote abundance in the absence of gray wolves but found the reverse pattern where wolf abundance was relatively high (Levi and Wilmers 2012; Newsome and Ripple 2015). Additionally, gray and red fox populations are likely declining in the Midwestern USA (Cooper et al. 2012; Lesmeister et al. 2015; Berry et al. 2017; Rich et al. 2018; Bauder et al. 2020) whereas coyote populations are increasing (Bauder et al. 2020). However, Crimmins and Van Deelen (2019) found relatively weak relationships between coyotes and foxes using abundance indices from Wisconsin. Similarly, Fowler et al. (2021) found no effect of coyote occupancy on red fox occupancy in northern Michigan where wolves were absent while Kellner et al. (2020) did not find a negative association between coyote and red fox abundance using observations by archery deer hunters across New York.

Inferring population-level effects of coyotes on foxes require considering the effect of spatiotemporal scale, because contrasting effects may appear when examined at broad and fine spatial extents (Sivy et al. 2017; Jachowski et al. 2020). Use of long-term data can reduce the effects of short-term demographic fluctuations (e.g., in response to fluctuating prey populations) that may obscure important long-term population-level patterns. Yet most studies evaluating the effects of coyotes on fox populations have occurred at relatively fine spatial extents or over short durations (but see Levi and Wilmers 2012; Newsome and Ripple 2015). However, fine-scale spatiotemporal avoidance may permit coexistence between coyotes and foxes across larger spatial extents (Wang et al. 2015; Clare et al. 2016;

Sivy et al. 2017; Rich et al. 2018), thereby obscuring population-level response across larger spatiotemporal extents. For example, urbanized landscapes may facilitate coexistence between sympatric canids by providing spatial refugia and food resources (Lesmeister et al. 2015; Rota et al. 2016; Moll et al. 2018; Mueller et al. 2018) Other forms of habitat heterogeneity (e.g., hardwood trees for gray fox escape cover; Lesmeister et al. 2015) or spatial partitioning based on resource availability (Robinson et al. 2014) may also permit local coexistence between coyotes and foxes. Alternatively, anthropogenic landscape alterations may also limit opportunities for spatiotemporal partitioning among sympatric canids (Morin et al. 2022). Consequently, it is important to investigate the population-level effects of coyotes on foxes using long-term data across broad spatial extents.

We used multiple long-term (up to 41 year) time series of red fox, gray fox, and coyote abundance indices collected across Illinois, USA, to test for effects of increasing coyote abundances on fox abundances. Previous research (Bauder et al. 2020) documented declines in abundance indices for both red foxes and gray foxes concurrent with increasing coyote trends. However, other unmeasured factors may have contributed to declining fox trends. For example, Illinois has lost approximately 81% of its native forest and 99% of prairie land cover since 1820 largely to agriculture (Iverson 1988; Walk et al. 2010). Since the 1950s, the majority of Illinois' agriculture has been dominated by corn [*Zea maeiza*] and soybean [*Glycine max*] with increasing farm sizes and declining hay, small grains, and pasture land use (Warner 1994; Walk et al. 2010; U.S. Department of Agriculture 2017). Such landscape changes may have reduced habitat availability and quality for gray and red foxes and potentially increased opportunities for coyotes to competitively exclude foxes (Goselink et al. 2003). Increasing agricultural intensification and declining pasture cover may also reduce prey abundance, particularly eastern cottontails (*Sylvilagus floridanus*) (Ribic et al. 1998; Mankin and Warner 1999; Nawrocki et al. 2019).

We used discrete-time Lotka-Volterra competition models (Levi and Wilmers 2012) to evaluate four a priori hypotheses regarding long-term variation in abundance of red and gray foxes: (1) increasing coyote abundances have depressed red and gray fox abundances, (2) changes to land cover and land use have reduced red and gray fox abundances, (3) variation in red and gray fox abundances is regulated by density-dependent population growth, and (4) variation in red and gray fox abundances is unaffected by these factors (i.e., a null model). We evaluated each of our hypotheses using empirical support for each candidate model. Previous long-term studies (e.g., Levi and Wilmers 2012; Newsome and Ripple 2015) documented top-down effects of coyotes on foxes through competitive exclusion and intraguild mortality. Thus, we predicted greater empirical support for our coyote suppression model than for all other hypotheses.

Methods

Study area

We used data collected throughout Illinois, USA during 1976–2018. Agriculture is the dominant land-cover type in Illinois followed by forest and urban land cover (62%, 15%, and 10% coverage, respectively, using 2001 National Land Cover Data accessed at <https://www.mrlc.gov> on 1 November 2019). The Chicago metropolitan area occurs in north-east Illinois, and row-crop agriculture is most prevalent in the northern and central parts of the state (Appendix S1; see Bauder et al. (2020) and Walk et al. (2010) for additional

descriptions of the study area). Elevation ranges from 85 to 380 m, mean monthly temperatures ranged from -3 to 24 °C, and mean monthly precipitation ranged from 5 to 12 cm (data accessed at <https://mrcc.illinois.edu/CLIMATE/> on 23 May 2019).

Archery deer-hunter observations

We used canid observations by from randomly selected archery deer hunters across Illinois. Hunters participating in the program received a record sheet in the mail prior to the start of the archery deer hunting seasons from 1992 to 2018. Hunters were asked to record observations of several species, including coyotes, gray foxes, and red foxes between 1 October and 14 November each year as well as the date of each hunting trip and daily effort (hours hunted) (Bauder et al. 2021b). We used the number of coyotes, gray foxes, and red foxes seen per 1000 hunter-observation hours as reported in annual reports from the Illinois Department of Natural Resources (Bauder et al. 2021a).

Trapper harvest data

We estimated harvest data from trappers using annual repeat-mail questionnaires (1975–2018) delivered to a random sample of license holders [except in 1976 when all licensed trappers ($n=17,800$) received a questionnaire]. Details regarding questionnaires, response rates, and trapping season dates, and durations are provided in Bauder et al. (2020). Trapping season lengths were identical for all three canid species, except for 1977 when the coyote season was 75 days and the fox season was 30 days and was typically open from mid-November through mid-January (Bauder et al. 2020). Trapping season length increased during our study from 30 days during 1978–1983 to 98 days during 2017–2018. Our three study species had no harvest limits and harvest regulations remained relatively constant during our study. We considered two harvest-based indices for our analyses: annual trapper harvest (hereafter total annual harvest, available statewide during 1976–2018) and per capita harvest (i.e., reported harvest per trapper from trappers harvesting at least one individual of a given species, available statewide from 1975 to 2018).

Covariates

We used three land-cover covariates to describe land-cover and land-use changes throughout Illinois: mean farm size, total cropland area, and total forest area. We obtained farm size and cropland area information from the United States Department of Agriculture's (USDA) Census of Agriculture using values collected every 4–5 years during 1974–2017 (U.S. Department of Agriculture 2017). To interpolate values for each year, we modeled statewide mean farm size and total cropland using linear regression models with quadratic and cubic polynomial effects of year, respectively, and Gaussian errors. These models had adjusted R^2 values of 0.90 and 0.68, respectively. Mean farm size and forest cover increased while total cropland cover initially declined from a peak around 1980 and increased slightly from a low around 2010 (Appendix S2). We used estimates of statewide total forest area from the U. S. Forest Service's Forest Inventory and Analysis (FIA) Program, which showed increasing forest cover during our study (Appendix S1; see also Walk et al. 2010). We obtained data values using the online tool EVALIDator (v. 1.8.0.01) using inventory years 1985, 1998, and 2003–2018.

We also obtained estimates from 1962 and 1948 although methodological differences between these first two years and subsequent years do not allow for direct comparison (S. Crocker, U.S. Forest Service, personal communication). However, we assumed that values from 1948 and 1962 would be sufficient for interpolating trends in Illinois statewide forest coverage during our study period. We interpolated statewide forest cover using a cubic polynomial model as described above (adjusted $R^2 = 0.90$).

Statistical analyses

We used the approach of Levi and Wilmers (2012) to test our hypotheses for relationships between fox indices and coyote indices and landscape covariates. This approach uses the discrete-time Lotka–Volterra competition equation:

$$n_{t+1} = n_t \times \exp(\beta_{n0} + (\beta_{n1} \times n_t) + (\beta_{n2} \times p_{1t}) + (\beta_{n3} \times p_{2t})) \quad (1)$$

where n is an index of abundance for the focal species, β_{n0} is the density-dependent effect of the focal species, and β_{n2} and β_{n3} are the inter-specific effects of species p_1 and p_2 , respectively, on the focal species. Taking the log of this equation results in

$$\ln(n_{t+1}) = \ln(n_t) + \beta_{n0} + (\beta_{n1} \times n_t) + (\beta_{n2} \times p_{1t}) + (\beta_{n3} \times p_{2t}) \quad (2)$$

$$\ln(n_{t+1}) - \ln(n_t) = r_n(t) = \beta_{n0} + (\beta_{n1} \times n_t) + (\beta_{n2} \times p_{1t}) + (\beta_{n3} \times p_{2t}) \quad (3)$$

Modeling $r_n(t)$ allows estimation of model parameters using a general linear model. We, therefore, calculated $r_n(t)$ for red foxes and gray foxes and fit the following model:

$$r_{FOX}(t) = \beta_0 + (\beta_{FOX} \times n_t) + (\beta_{Covariate} \times X_{1t}) \quad (4)$$

where β_{FOX} represents the density-dependent effects of fox, X was one of our covariates (an index of coyote abundance, cropland area, mean farm size, forest area), and n was an index of abundance for one fox species. We z -score standardized all covariates (i.e., n and X) prior to model fitting.

For each fox species we fit six candidate models, one for each of our four covariates, one including only a density-dependent effect of fox, and one including only the intercept (β_0 ; i.e., a null model). We added a value of one to all harvest-based indices for gray fox to avoid having a value of zero during 2015 when no gray fox harvest was reported. We included covariates in separate models because of collinearity among covariates (Appendix S3) and the relatively limited number of years in our time series. However, because collinearity between coyote abundance and landscape covariates was moderate ($|r| = 0.51–0.56$) for our archery observations, we conducted a post hoc analysis using these data for each fox species to explore more complex models. Specifically, we fit three additional models each containing a coyote and landscape effect (i.e., coyote + farm size, coyote + cropland, coyote + forest). Variance inflation factors from these three models were ≤ 5.13 . We fit models using the lm function in R and used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002) to calculate AIC_c model weights (w) as a means of evaluating the empirical support for each hypothesis (i.e., model). We also report the covariate coefficients and 95% CI as measures of strength for each covariate.

Results

We documented positive trends in abundance indices for coyotes and generally negative trends for red foxes and gray foxes statewide (Fig. 1). Coyote indices were negatively correlated with their respective indices for red fox and gray fox with the strongest, albeit moderate, relationship for archery indices (red fox: $r = -0.32$; gray fox: $r = -0.36$) followed by total annual harvest (red fox: $r = -0.21$; gray fox: $r = -0.22$). Correlations were weakest for per capita harvest (red fox: $r = -0.12$; gray fox: $r = -0.01$). Coyote indices were most correlated with landscape covariates for per capita harvest ($|r| \geq 0.81$), followed by archery hunter observations ($|r| = 0.51-0.56$), and total annual harvest ($|r| = 0.33-0.71$;

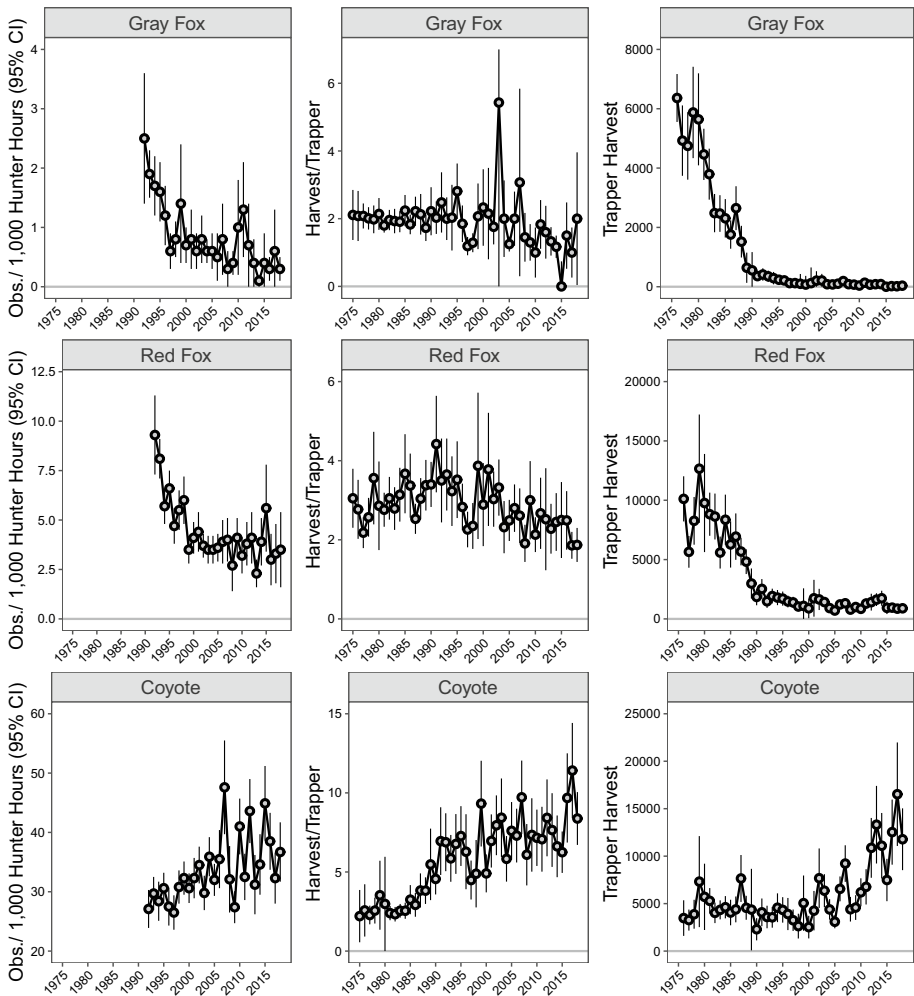


Fig. 1 Trends in red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), and coyote (*Canis latrans*) abundance indices in Illinois, USA using statewide estimates from archery deer-hunter observations (Obs./1000 Hunter Hours), per capita trapper harvest (Harvest/Trapper), and annual trapper harvest (Trapper Harvest) during 1975–2018. Points are observed index values and error bars are 95% CI

Appendix S3). Collinearity among landscape covariates was most variable concurrent with our archery hunter observations ($|r|=0.51\text{--}0.99$) and least variable concurrent with both harvest-based indices ($|r|=0.80\text{--}0.94$; Appendix S3).

Red fox

Our coyote hypothesis received greatest support ($w=0.58$) for statewide archery observations of red foxes but received only 1.6 times the support as the farm size ($\pi=0.37$) hypothesis (Fig. 2). The 95% CI of both covariates were less than zero (coyote: $\beta = -0.17$,

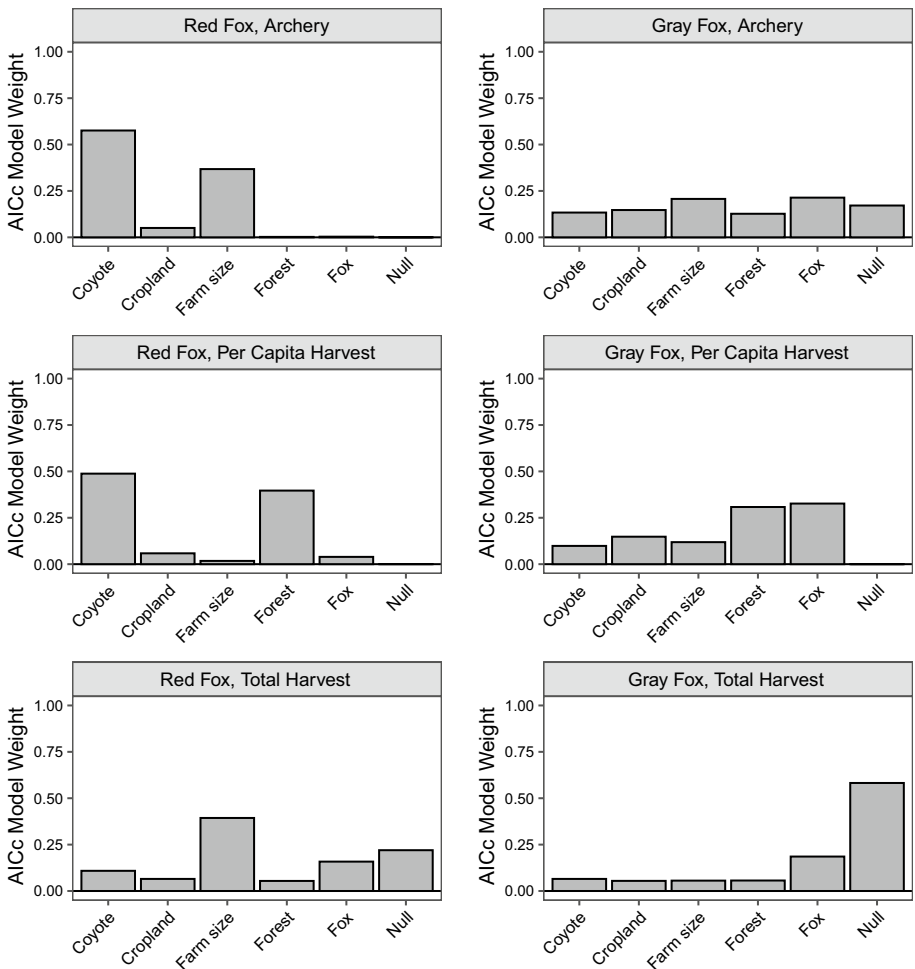


Fig. 2 Akaike’s Information Criterion adjusted for small sample sizes (AIC_c) model weights (w) for Lotka–Volterra models of population growth for red fox (*Vulpes vulpes*) and gray fox (*Urocyon cinereoargenteus*) archery deer-hunter observations, total annual trapper harvest, and per capita trapper harvest across Illinois, USA, during 1975–2018. Candidate models include an index of coyote (*Canis latrans*) abundance of the same data type as the response variable (Coyote), total cropland area (Cropland), mean farm size (Farm size) forest area (Forest), fox density dependence (Fox), and a null (i.e., intercept-only) model

95% CI -0.26 to -0.08 ; farm size: $\beta = -0.30$, 95% CI -0.46 to -0.13 ; Table 1). Our coyote hypothesis also received greatest support ($w=0.49$) for statewide per capita harvest but received only 1.2 times the support as the forest hypothesis (Fig. 2). The 95% CI of both covariates were less than zero (coyote: $\beta = -0.07$, 95% CI -0.13 to -0.02 ; forest: $\beta = -0.09$, 95% CI -0.15 to -0.02 ; Table 1). The farm size hypothesis received the greatest support ($w=0.39$) for total annual harvest, but this model had only 1.8 times the support of the null (i.e., intercept-only) model and 2.5 times the support of the density dependence model (Fig. 2). The 95% CI of the coefficient for mean farm size was less than zero ($\beta = -0.25$, 95% CI -0.50 to -0.003 ; Table 1). Coefficient estimates for the density dependence effects (i.e., z-score standardized red fox abundance at $t-1$) were consistently higher than the coefficients for coyote abundance and landscape covariates (Table 1; Appendix S4). Our post hoc analysis revealed that our model with an effect of coyote abundance and farm size had approximately 2.8 times the empirical support as the model with only coyote abundance ($w=0.52$ vs. 0.18, respectively; Appendix S5) and indicated negative effects of both covariates (farm size: $\beta = -0.19$, 95% CI -0.36 to -0.01 ; coyote: $\beta = -0.11$, 95% CI -0.21 to -0.02 ; Appendix S5).

Gray fox

Three models received 59% of the empirical support for statewide archery observations of gray foxes (Table 1). The density dependence hypothesis had the most empirical support ($w=0.21$), but this support was similar to that of the farm size hypothesis ($w=0.21$) and the null model ($w=0.17$; Fig. 1). There was evidence of a negative effect of farm size on archery observations of gray fox ($\beta = -0.30$, 95% CI -0.70 to 0.09 ; Table 1). Similarly, the density dependence hypothesis had the most empirical support ($w=0.33$) for statewide per capita harvest of gray foxes with similar empirical support for the forest hypothesis ($w=0.31$). These models had about twice the empirical support as the third-ranked hypothesis, the cropland hypothesis ($w=0.15$; Table 1). There was evidence of a negative effect of forest cover on per capita harvest of gray foxes ($\beta = -0.06$, 95% CI -0.15 to 0.02 ; Table 1). The null model received the greatest support ($w=0.58$) for total annual harvest of gray foxes and had 3.1 times the empirical support as the density dependence hypothesis (Table 1). Coefficient estimates for the density dependence effects (i.e., z-score standardized red fox abundance at $t - 1$) were consistently higher than the coefficients for coyote abundance and landscape covariates (Table 1; Appendix S4). Our post hoc analysis revealed that our combined coyote and landscape models had the lowest empirical support (Appendix S6).

Discussion

Our results reveal ambiguity in long-term relationships between indices of abundance for sympatric canids, particularly gray foxes. Both red fox and gray fox populations exhibited declines across all three abundance indices while coyote abundance increased, yet correlations between fox and coyote indices were relatively low across all three data types. More importantly, our coyote hypothesis often received equivocal (red foxes) or less support (gray foxes) than our other models and the coefficient estimates for fox density-dependent effects were consistently stronger than the coefficients for coyote effects. Even for red fox archery hunter observations and per capita harvest, where the coyote hypothesis received

Table 1 Models ranked by AICc weight (*w*) for Lotka–Volterra models of population growth for red fox (*Vulpes vulpes*) and gray fox (*Urocyon cinereoargenteus*) archery deer-hunter observations, total annual trapper harvest, and per capita trapper harvest across Illinois, USA, during 1975–2018

Red fox			
Archery hunter observations			
Model	<i>w</i>	Fox	Covariate
Fox + Coyote	0.576	-0.205 (-0.295 to -0.115)	-0.166 (-0.255 to -0.078)
Fox + Farm	0.368	-0.409 (-0.577 to -0.242)	-0.295 (-0.460 to -0.130)
Fox + Crop	0.050	-0.342 (-0.505 to -0.178)	0.228 (0.067 to 0.389)
Fox	0.003	-0.153 (-0.260 to -0.045)	
Fox + Forest	0.002	-0.209 (-0.344 to -0.073)	-0.095 (-0.237 to 0.048)
Null	0.000		
Gray fox			
Archery hunter observations			
Model	<i>w</i>	Fox	Covariate
Fox	0.214	-0.203 (-0.447 to 0.041)	
Fox + Farm	0.207	-0.452 (-0.851 to -0.052)	-0.303 (-0.696 to 0.089)
Null	0.171		
Fox + Crop	0.147	-0.393 (-0.766 to 0.020)	0.245 (-0.123 to 0.613)
Fox + Coyote	0.134	-0.260 (-0.518 to 0.003)	-0.161 (-0.415 to 0.093)
Fox + Forest	0.127	-0.340 (-0.668 to 0.012)	-0.213 (-0.559 to 0.133)
Per capita trapper harvest			
Model	<i>w</i>	Fox	Covariate
Fox + Coyote	0.489	-0.109 (-0.163 to -0.055)	-0.074 (-0.128 to -0.020)
Fox + Forest	0.397	-0.141 (-0.202 to -0.079)	-0.085 (-0.149 to -0.021)
Fox + Crop	0.058	-0.120 (-0.180 to -0.060)	0.052 (-0.007 to 0.112)
Fox	0.039	-0.103 (-0.161 to -0.045)	
Fox	0.327	-0.185 (-0.264 to -0.105)	
Fox + Forest	0.308	-0.206 (-0.290 to -0.122)	-0.064 (-0.152 to 0.023)
Fox + Crop	0.148	-0.190 (-0.271 to -0.109)	0.036 (-0.045 to 0.116)
Fox + Farm	0.119	-0.188 (-0.269 to -0.107)	-0.025 (-0.105 to 0.056)

Table 1 (continued)

Per capita trapper harvest		Per capita trapper harvest	
Model	w	Covariate	Covariate
Fox + Farm	0.018	Fox -0.107 (-0.166 to -0.048)	Fox + Coyote -0.026 (-0.084 to 0.033)
Null	0.000		Null
Trapper harvest			
Model	w	Covariate	Covariate
Fox + Farm	0.394	Fox -0.295 (-0.544 to -0.046)	Null -0.250 (-0.497 to -0.003)
Null	0.220		Fox -0.028 (-0.331 to 0.274)
Fox	0.158	-0.063 (-0.163 to 0.037)	Fox + Coyote -0.046 (-0.358 to 0.266)
Fox + Coyote	0.109	-0.075 (-0.176 to 0.027)	Fox + Forest 0.010 (-0.418 to 0.438)
Fox + Crop	0.065	-0.129 (-0.326 to 0.067)	Fox + Farm -0.131 (-1.137 to 0.874)
Fox + Forest	0.054	-0.091 (-0.238 to 0.055)	Fox + Crop 0.055 (-0.560 to 0.521)

Coefficient estimates and 95% confidence intervals are reported for Fox and the second covariate within each model, with models whose 95% CI for the second covariate exclude zero noted in bold. Covariates include mean farm size, total cropland area, forest area, and an index of coyote (*Canis latrans*) abundance of the same data type as the response variable. The covariate Fox is the index of the response variable at year $t - 1$

the greatest support, landscape hypotheses had relatively similar levels of empirical support. However, in both of these cases, the estimated coyote effect on red foxes was negative, and the 95% CI excluded zero. Moreover, our post hoc analyses still detected a relatively strong negative effect of coyote abundance while controlling for landscape changes (i.e., mean farm size). Despite the challenges of inferring inter-specific effects using broad-scale correlative studies, our results highlight the importance of considering multiple potentially causal mechanisms when attempting to infer reasons behind population trends.

Our results are partially consistent with those of previous long-term studies documenting negative effects of coyotes on foxes where gray wolves were absent or not abundant (Levi and Wilmers 2012; Newsome and Ripple 2015). In particular, Levi and Wilmers (2012) found that strong evidence of coyote suppression of foxes in southern Minnesota where wolves were absent. Newsome and Ripple (2015) also reported that coyote fur returns were greater than red fox fur returns in rangeland and agriculturally dominated landscapes of south-central Canada where wolves were absent. Landscape differences may have contributed towards the apparent discrepancy between our findings and past results, as our study area was highly modified by agriculture and urbanization compared to less disturbed landscapes used in these previous two studies (Levi and Wilmers 2012; Newsome and Ripple 2015). Our study area was also at a lower latitude than previous studies (Levi and Wilmers 2012; Newsome and Ripple 2015) and latitudinal variation in climate may affect the strength of intraspecific interactions, our ability to detect such interactions, or both. However, ecological theory often predicts stronger biotic (e.g., competitive) effects on inter-specific interactions at lower latitude (Sirén and Morelli 2020) further complicating efforts to understand latitudinal variation in inter-specific canid interactions.

Our landscape change hypotheses were often competitive, suggesting that landscape changes had some influence on fox trends, particularly for red fox. While our study cannot elucidate the causal mechanism underlying the negative relationship between red foxes and mean farm size, this relationship could reflect a loss of natural habitat patches (e.g., woodlots) for foxes and/or their prey (Ribic et al. 1998; Mankin and Warner 1999; Nawrocki et al. 2019). It may also reflect increased potential for negative competitive interactions between coyotes and foxes within remaining natural habitat patches (Gosselink et al. 2003; Morin et al. 2022). Coyotes also had negative effects on foxes in human-modified landscapes in southern Minnesota (Levi and Wilmers 2012). Yet canid inter-specific interactions can vary across spatiotemporal scales (Clare et al. 2016; Shores et al. 2019) and pooling data across heterogeneous landscape, as in our statewide analyses, could, therefore, mask regional variation in canid inter-specific interactions. Land-cover composition differs markedly between the northern and southern halves of Illinois, with approximately 68% agriculture, 12% urban, and 10% forest in the north and 56% agriculture, 21% forest, and 10% grassland/pasture in south (2001 National Land Cover Data available at www.mrlc.gov).

The support for the coyote hypothesis was greatest for red foxes where there was a clear negative effect of coyote for both archery hunter observations and per capita harvest. Coyotes are known to negatively affect red foxes through intraguild predation (Sargeant and Allen 1989; Gosselink et al. 2007) and spatiotemporal avoidance (Harrison et al. 1989; Randa and Yunker 2006). Although such fine-scale avoidance may not necessarily lead to population-level effects, there is evidence of substantial red fox declines in Illinois (Lesmeister et al. 2015; Berry et al. 2017) and the Midwest as a whole (Lesmeister et al. 2015; Rich et al. 2018). An alternative hypothesis for a negative relationship between coyotes and red foxes is a shift towards red foxes using more urbanized areas (Gosselink et al. 2003) which in turn may create a “human shield” from coyotes (Moll et al. 2018). While both

red foxes and coyotes are capable of using habitats across a wide range of urbanization levels (Gehrt and Riley 2010; Soulsbury et al. 2010; Mueller et al. 2018), such urban refuge may mitigate negative population-level response to coyotes for red foxes (Lesmeister et al. 2015). Such a shift may also create bias in our indices as urban areas are not frequented by archery deer hunters or trappers, thereby lowering their probability of encountering foxes. Leveraging additional observation datasets (e.g., citizen science, urban camera-trap studies; Fidino et al. (2021)) and fine-scale telemetry datasets (e.g., known-fate mortality, habitat selection) across urban areas may help better evaluate a hypothesized shift to urban areas by red foxes. The farm size model received the most support for red fox trapper harvest yet we recommend caution when drawing inference from this result as trapper harvest was not adjusted trapper numbers which declined markedly during our study (Bauder et al. 2020).

In contrast to red foxes, our coyote hypothesis received virtually no empirical support across all three gray fox indices similar to a nationwide study of gray fox occupancy using camera traps (Allen et al. 2022). Coyotes can kill and competitively exclude gray foxes (Fedriani et al. 2000; Chamberlain and Leopold 2005; Farias et al. 2005), and Egan et al. (2021) reported broad-scale negative relationships between coyote and gray fox occupancy across Eastern North America. It is, therefore, unclear why we failed to detect a stronger negative effect of coyotes on gray foxes in Illinois given the evidence for gray fox declines in the Midwest (Cooper et al. 2012; Lesmeister et al. 2015; Rich et al. 2018). Gray foxes can also use urban environments (Allen et al. 2021) and may also potentially use urban areas as “human shields” to avoid coyotes (Lesmeister et al. 2015; Wang et al. 2015). Morin et al. (2022) found no evidence of avoidance among coyotes and gray foxes in southern Illinois but hypothesized that widespread, albeit moderate, human landscape disturbance limited opportunities for spatiotemporal avoidance. Within eastern North America, gray foxes are generally associated with forests (Cooper et al. 2012; Lesmeister et al. 2015) and their response to urbanization varies across studies (Allen et al. 2021). Gray foxes are also capable climbers (Fritzell and Haroldson 1982), and availability and use of escape cover may mediate the effects of coyotes on gray foxes (Lesmeister et al. 2015). The low support for our coyote hypothesis for gray foxes may also reflect our analysis of statewide trends whereas both forest cover and gray fox abundance are greater, which are southern Illinois (Cooper et al. 2012). Finally, the greater support for the null model for gray fox trapper harvest may also reflect a general unsuitability of this index due to its confounding with trapper numbers (Bauder et al. 2020).

Our analytical approach has been used in previous studies of inter-guild interactions among canids (Levi and Wilmers 2012). However, our study, along with those previous studies, has generally not considered observation error (Levi and Wilmers 2012; Newsome and Ripple 2015) nor has not fully propagated uncertainty in estimates of abundance (Crimmins and Van Deelen 2019). While we believe that our results provide valuable insight into the population ecology of sympatric canids, the extent to which our results may be biased by these two shortcomings is not fully understood. The consequences of these two factors in estimating inter-specific interactions from long-term datasets are also unclear. The Lotka–Volterra model used in our study could be fit in a state-space modeling framework to account for observation error, and we encourage future simulation studies to explore this topic as part of a larger effort to develop robust analytical methods to account of observation error within long-term datasets while also propagating uncertainty in resulting estimates.

Our results provided support for the hypotheses that increasing coyote populations and/or changing landscapes are causal mechanisms for declining red fox and gray fox trends in the Midwestern USA. However, the equivocal support among multiple ecological mechanisms

combined with high covariate collinearity and relatively short time series illustrates the challenges of inferring the mechanisms behind broad-scale population trends using correlative studies. Our results highlight the need for additional research to better understand how negative individual-level interactions between foxes and coyotes may translate into population-level responses, and other potential mechanisms influencing fox declines (e.g., disease, changing prey communities), while accounting for the inherent differences in the ecology of fox species. Additional population monitoring of red foxes and gray foxes using sampling methods that are robust to potential behavioral shifts (e.g., camera traps across rural–urban gradients and a variety of habitats) and that allow for the analytical control of factors contributing to sources of observation error (e.g., diverse sources of imperfect detection, Nichols et al. 2009) may provide these insights. Finally, we encourage simulation-based studies evaluating the accuracy of state-space models accounting for observation error and fully propagating parameter uncertainty when inferring inter-specific relationships from long-term datasets.

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Data availability The data and R script used during this current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict or competing interests.

Ethical approval All research was approved by the University of Illinois' Institutional Review Board (IRB 10236).

Consent to participate Not applicable.

Consent for publication Not applicable.

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