Check for updates

Received: 3 March 2020 | Accepted: 15 January 2021

DOI: 10.1111/1365-2435.13765

RESEARCH ARTICLE

Functional Ecology BRITISH ECOLOGICAL SOCIETY

Quantifying temporal variation in dietary niche to reveal drivers of past population declines

Amanda E. Cheeseman | Brian P. Tanis | Elmer J. Finck

Department of Biological Sciences, Fort Hays State University, Hays, KS, USA

Correspondence
Amanda E. Cheeseman
Email: acheesem@esf.edu

Present address
Amanda E. Cheeseman, Department of Environmental and Forest Biology, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210, USA

Brian P. Tanis, Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, USA

Funding information
Kansas Department of Wildlife, Parks, and Tourism, Grant/Award Number: 228642

Handling Editor: Angélica Gonzalez

Abstract

1. Given the long and dynamic history of anthropogenic disturbances to ecosystems, it is difficult to determine the drivers of past population declines. These uncertainties dilute the efficacy of conservation efforts and might hinder species and ecosystem recovery.
2. Niche quantification can be a useful tool for understanding drivers of past population declines. Niche parameters reflect key resources used, providing insight into the conditions needed to achieve population stability. By reconstructing a population's niche position and space over a period of decline and comparing to historic baselines, shifts in the realized niche of a species can be assessed. Comparing shifts to historic information on resource availability and timing of declines can allow practitioners to identify probable drivers of species decline.
3. We demonstrated the utility of this technique by reconstructing parameters of isotopic dietary niche over a 130-year period and comparing isotopic niche reconstructions to land use and crop harvests during this same period via regression and Bayesian standard ellipsoid (SIBER) analyses. We use a formerly widespread but now endangered species, the eastern spotted skunk *Spilogale putorius*, addressing the hypothesis that land use change and agricultural intensification led to a historical collapse of key dietary resources which correlates with population declines in this species. To help control for isotopic variability unrelated to population decline, we compare trends to those of a secure, but ecologically similar generalist mesocarnivore, the striped skunk *Mephitis mephitis*, across the same spatiotemporal scale.
4. We present evidence that historic dietary changes occurred in spotted skunks in the early 1900s but not to the same degree in striped skunks. Changes in isotopic composition correspond with the temporal period of decline and are explained by concurrent changes in land use. These results support the hypothesis that loss of key dietary resources as a result of land use change and agricultural intensification played a significant role in population declines of spotted skunks in this region.

KEYWORDS
agriculture, historical ecology, land use, *Mephitis*, mesocarnivore, skunk, *Spilogale*, stable isotope

1 | INTRODUCTION

Anthropogenic disturbances have profound impacts on species ecology and have resulted in unprecedented rates of population decline and species extirpation (Ceballos et al., 2015; Lewthwaite et al., 2017; Seebens et al., 2017; Urban, 2015). While this leaves little doubt that human activities have detrimental consequences for species, it is challenging to pinpoint the primary mechanisms driving population declines. This is especially true for species that faced historical disturbances as our knowledge of the system is limited by the availability of historical records while our frame of reference is subject to shifting baselines (Papworth et al., 2009). These factors obscure the underlying causes for species loss and present major hurdles for conservation managers (Newsome et al., 2007; Peterson et al., 2006; Scheele et al., 2017).

One potential method for understanding population declines is to quantify changes in a species' niche. Representing the totality of the biotic and abiotic interactions encompassed by a species, the niche provides a useful framework for identifying critical conditions and resources necessary for survival and reproduction (Cadotte, 2004). Quantifying alterations in the position and shape of the niche over temporal or spatial scales can reveal otherwise hidden attributes contributing to population decline (Manlick et al., 2019; Rossman et al., 2016; Swanson et al., 2015; Yeakel et al., 2013). For example, reduced availability of critical resources might be evidenced by an increase in intraspecific variation in niche space for generalist species as alternative resources are used (Korotkevich et al., 2018; Svanback & Persson, 2004; Wilson & Turelli, 1986).

While it is impossible to quantify the n-dimensions representing a species' Hutchinsonian niche, the isotopic niche has become a widely cited reflection of this hypervolume (Chase & Leibold, 2003), allowing for detailed studies comparing how populations and species interact with and persist in their environments (Newsome et al., 2012). Stable isotope analysis (SIA) measures the ratios of different isotopes for specific elements within organic tissues in the context of ecological and environmental factors. This technique makes use of variation in the isotopic signal of the resources consumed (Koch et al., 2017; Newsome et al., 2012), as well as predicable patterns of fractionation in stable isotopes that occur in the body as biochemical processes turn food into tissue (Roth & Hobson, 2000). Thus, SIA captures aspects of both the biotic and abiotic components that enable a species to persist at a location, which serves as a quantifiable reflection of an organism's niche space. Furthermore, SIA can be performed on a variety of inert organic tissues (e.g. hair and bone), which can be sampled from historical museum specimens. This enables quantification of isotopic niche within past ecosystems, offering a method to measure and provide context to broad-scale changes in species ecology (Green & Scharlemann, 2003; Shaffer et al., 1998). Such examination of isotopic niche over time has been useful for identifying drivers of population changes in numerous systems including invertebrates (Jackson et al., 2012; Olsson et al., 2009), fish (Feiner et al., 2013; Guzzo et al., 2013; Layman et al., 2007), birds (Chamberlain et al., 2005; English et al., 2018) and mammals (Han et al., 2019; Szteren et al., 2018).

Among anthropogenic causes of species decline, conversion of land for agriculture is consistently ranked among the top drivers of species endangerment globally (Czech et al., 2000; Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019). The negative impacts of agriculture stem from multiple sources, including habitat loss and fragmentation (Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019), agricultural intensification (Donald et al., 2001), increased human–wildlife conflict (Nyhus, 2016) and the use of pesticides and fertilizers (Brühl et al., 2013; Mineau & Whiteside, 2013; Sánchez-Bayo & Wyckhuys, 2019). While overall impacts of agricultural land use on species are well documented, the ecosystem-level impacts are less clear. Agricultural land use shifts resource availability at the base of trophic networks (i.e. primary producers and insects), leading to bottom-up trophic effects known to trigger population fluctuations and can result in species loss (Donald et al., 2001; Kagata & Ohgushi, 2006; Muhly et al., 2013). For example, pesticides and fertilizers have been implicated in global insect declines (Sánchez-Bayo & Wyckhuys, 2019), which have had cascading effects resulting in altered trophic positioning and population declines in vertebrates (English et al., 2018).

Conversely, as agricultural systems encroach upon native habitats, cultivated food subsides can provide an easily accessible, high-quality energy source to wildlife, which might replace or be selected for over natural prey (Boggie et al., 2018; Magioli et al., 2014). The potential for such subsidies to have population-level impacts is recognized such that planting cereals and other agricultural food crops is recommended widely to promote populations of waterfowl and has had demonstrated success in increasing fitness and population size (Fox et al., 2017; Ringelman, 1990; Sedinger & Alisauskas, 2014).

Herein, we demonstrate the utility of using reconstructions of isotopic niche alongside historic and contemporary land use and population data to infer the causes for population decline. We use the eastern spotted skunk *Spilogale putorius* (hereafter spotted skunk) as a case study, given the uncertainty surrounding range-wide declines in the early-mid 20th century, including a hypothesized link between declines and collapse of a primary food source due to land use change (Choate et al., 1973; Gompper & Hackett, 2005). We examine how a century of land use change influenced the isotopic niche of spotted skunks and compare these trends to those of another generalist mesocarnivore of similar body size, the striped skunk *Mephitis mephitis*, which did not experience the same magnitude of decline. We specifically tested the hypothesis that declines of spotted skunks were linked to a change in available resources as agricultural practices changed and intensified throughout the early 20th century. To accomplish this, we assessed the following: (a) changes in land use from 1880 to 2007, (b) the timing, magnitude and duration of population decline for spotted and striped skunks using harvest as an indicator, (c) the relationship between spotted and striped skunk harvest and land use changes, (d) isotopic composition of spotted and striped skunks in response to land use change and the period of decline and (e) changes in isotopic niche space relative to the period of decline, comparing the presence and magnitude of isotopic niche parameter changes between species.

2 | MATERIALS AND METHODS

2.1 | Study system

As a result of population declines, the spotted skunk is a species of conservation interest and the plains subspecies (*S. putorius interrupta*) is being considered for listing on the United States Endangered Species Act (USFWS, 2012). As a generalist predator with a large geographical range, declines are unexpected (Gompper & Hackett, 2005). Ecologically similar species, like the striped skunk, experienced minor population declines but are considered secure (Helgen & Reid, 2016; Landholt & Genoways, 2000; Leopold, 2010). Habitat and land use change, overharvest, disease and the introduction of synthetic pesticides have been hypothesized as drivers of declines (Choate et al., 1973; Gompper & Hackett, 2005). However, the timing and spatial distribution of decline are inconsistent with outbreaks of known diseases and the introduction of synthetic pesticides as primary drivers of population decline (Gompper & Hackett, 2005). Similarly, low pelt price and a poor correlation between pelt price and harvest suggest take of spotted skunks is primarily incidental in the pursuit of other target species and not sufficient to implicate over-harvesting as a driver of decline (Gompper & Hackett, 2005; Sasse & Gompper, 2006). Another hypothesis is that the dynamic history of spotted skunks is tied to agricultural practices; yet, it is unclear if agricultural changes could explain these rapid, range-wide declines (Gompper & Hackett, 2005). Reports indicate that spotted skunks were uncommon throughout much of the Great Plains until the late 1800s, but the spread of early agriculture resulted in abundant food and cover resources in the form of field crops, stored harvest and commensal small mammals, all of which presumably facilitated rapid population growth and a northward range expansion (Choate et al., 1973). The later loss of these resources, as agricultural practices changed and intensified through the early-mid 1900s, has been proposed as a primary mechanism in spotted skunk decline, but this hypothesis has not been examined previously.

For both species, small mammals, arthropods and corn have been reported as major diet items (Crabb, 1941; Kelker, 1937; Selko, 1937); changes in the availability of these resources could mediate populations through bottom-up forces. Arthropods have declined generally in response to agricultural practices (Sánchez-Bayo & Wyckhuys, 2019), while trends in corn availability over time are more complex. In Kansas, the amount of land planted in corn decreased by millions of hectares between 1920 and 1930 (United States Census of Agriculture). At the same time, the combined use of fertilizers, pesticides and clean farming practices have increased crop yields, but might result in lower abundance of prey species and reduced accessibility. Here we made use of long-term population estimates, land use trends and quantifications of isotopic niche to address our hypothesis. As a geographical area with thorough historical records and the greatest number of specimens, we focused our data collection to Kansas, USA.

2.2 | Land use

We compiled county level United States Census of Agriculture statistics (1890–2007) to assess land use trends. We used average farm size and proportion of total land area in active cropping (hereafter "agriculture") as correlates of agricultural intensity (Guerrero et al., 2011; Mineau & Whiteside, 2013) where proportion of total land area in cropping describes the landscape-level abundance of cropland and average farm size describes the aggregation of smaller, diversely planted family and substance farms into larger farms planted in fewer, often high yield crops. Most agricultural crops common to the Great Plains (e.g. wheat, hay, oats and flaxseed) have C_3 photosynthetic pathways and, as a result, are characterized by low $\delta^{13}C$ values. Corn is a common exception with high $\delta^{13}C$ values due to its C_4 photosynthetic pathway. Corn and corn derivatives are commonly consumed by wildlife, including skunks, and are often identified in the isotopic niche (Alisauskas & Hobson, 1993; Murray et al., 2015; Newsome et al., 2010; Wassenaar & Hobson, 2000). Thus, given the potential importance and detectability of corn as a primary food source, we also compiled data on the proportion of total land area actively farmed in corn (hereafter "corn").

2.3 | Population trends

To establish baseline population trends for both skunk species, we examined effort corrected fur harvest records (Gompper & Hackett, 2005; Leopold, 2010; Sasse & Gompper, 2006). Harvest data are often used to infer historic population trends; however, we note that these data, in part, represent the number of pelts sold within the state and may not be proportional to the number of animals killed within the state. We compiled all available harvest data on striped (1928–2011) and spotted skunks (1928–1978), alongside pelt price, the number of licenses sold and trapping season length from publications of the Kansas Fish and Game Commission and the United States Fish and the Wildlife Service Wildlife Leaflets Series. Pelt prices for Kansas were only available for 1961–1979 so pelt prices from a neighbouring state (Missouri) were used from 1928 to 1960. All prices were adjusted for inflation using the consumer price index (United States Department of Labor, Bureau of Statistics, www.BLS.gov). Annual effort was estimated by multiplying season length by the number of licenses sold each year. We modelled harvest for each species as a function of pelt price, effort and year using a generalized linear model with a Gamma distribution for the residuals and a log link function via the glm function in Program R (Bolker, 2008; R Core Team, 2019). For both species, we assessed state-level correlations between predicted harvest and corn, agriculture and farm size using Spearman rank correlations and adjusted for multiple comparisons using Bonferroni corrections.

2.4 | Stable isotope analysis

To assess dietary change, we sampled all available adult spotted and striped skunks from museum collections and supplemented samples with opportunistic road collections. We sampled guard hairs, which remain biochemically unchanged after the period of growth, thus permitting analysis during the same seasonal window (i.e. August through October) for all skunks (Gannes et al., 1998). Guard hairs in the same growth phase were plucked from the dorsal surface of the skin, immediately anterior to the pelvic girdle then washed in chloroform for 24 hr. Multiple hairs from each individual were cut into 5 mm sections, homogenized, and 0.4 mg of sample was placed into tin capsules. Samples were then analysed for carbon (^{13}C) and nitrogen isotopes (^{15}N) using a GV Instruments Isoprime mass spectrometer with a Costech elemental analyzer (Raymond W. Lee lab, Washington State University, Pullman, WA, USA). All stable isotope data were reported in per mil notation ($\delta X = [R_{sample}/R_{standard}) - 1] \times 1,000$, where R is the stable isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Instrument precision was ±0.02‰ for $\delta^{13}C$ and ±0.00‰ for $\delta^{15}N$ based on the repeated measure of 29 in-house standards (albumin; $\delta^{13}C$: −16.3‰, $\delta^{15}N$: 3.87‰). Repeated analysis of hair samples indicated sampling variability of 0.50‰ ± 0.49‰ for $\delta^{13}C$ and 0.75‰ ± 0.71‰ for $\delta^{15}N$. We focused on these commonly used isotopes as they reflect variation in the value of the baseline resources consumed as well as predictable patterns of fractionation of stable isotopes that occur within an animal's body as biochemical processes turn food into tissue (Fox-Dobbs et al., 2007; Urton & Hobson, 2005). Specifically, $\delta^{13}C$ values reflect the photosynthetic pathways of the primary producers at the base of food webs, here C_3 and C_4 plants (C_3 mean = −27‰ range: −35‰ to −22‰; C_4 mean = −13‰ range: −14‰ to −10‰;) with minor fractionation as it is incorporated into mammalian hairs (1.6‰), and $\delta^{15}N$ values increase by ~3.8‰ with each increase in trophic level (Hobson & Quirck, 2014; Matson et al., 2012). Isotopic values for carbon were standardized to the year 1900 following Terry (2018) to account for the atmospheric shift in $\delta^{13}C$ values due to burning of fossil fuels (i.e. the Suess Effect, Keeling, 1979).

2.5 | Isotopic shifts

We used all subsets regression and an information theoretic approach to examine directional changes in each $\delta^{13}C$ and $\delta^{15}N$ values through time by species and in response to agriculture, average farm size and corn. Interactions between corn and farm size, species and all land use variables, and the three-way interaction of species × corn × farm size were also considered. If changes in $\delta^{13}C$ and $\delta^{15}N$ values corresponded to species declines, we predicted the relationship between year and isotope parameters would be nonlinear over the period of investigation, as such we also considered the quadratic effect of year. Finally, to control for the effects of aridity on carbon and nitrogen isotope values of plants, we also considered the variables precipitation and temperature (Ambrose, 1991; Diefendorf et al., 2010). Daily precipitation and maximum daily temperature were obtained from the nearest weather station to the georeferenced location for each specimen using the RNOAA package in Program R and averaged over the period of hair growth (Chamberlain, 2019). We assessed violations of model assumptions for the global model by examining residuals against fitted values, testing for outliers, and for multicollinearity using variance inflation factors for the global model without interactions. We used Akaike Information Criterion corrected for sample size (AIC_c) to evaluate models and considered models with a $\Delta AIC_c \leq 2.0$ to have support (Burnham & Anderson, 2002). We assessed the fit and explanatory power of the models by including an intercept-only null in each candidate model set and using adjusted R^2. Inferences were made based on model-averaged predicted values, averaged across all models and calculated using the AICCMODAVG package in program R (Arnold, 2010; Burnham & Anderson, 2002; Cade, 2015; Mazerolle, 2020).

2.6 | Isotopic niche breadth

Both spotted and striped skunks were binned a priori into three treatment groups in reference to periods when spotted skunks populations in Kansas were thought be stable or increasing (≤1925), declining (1926–1944) and after populations roughly stabilized post-decline (≥1945; Choate et al., 1973). Isotopic values for both species and treatment bins were plotted in a bivariate δ-space, with the reconstructed isotopic niche space calculated by using SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.4 (Jackson et al., 2011) to produce Bayesian standard ellipse areas (SEA_b). The SEA_b were compared across bins and changes in niche breadth inferred based on overlap of the Bayesian credible intervals (Arnold, 2010; Cumming & Finch, 2015; Hespanhol et al., 2019).

3 | RESULTS

3.1 | Land use

The percent of each county planted in corn declined abruptly between the 1930 and 1934 census (13.3 ± 9.3% to 6.6 ± 7.2%, respectively; Figure 1). Declines continued until 1969 (2.8 ± 4.1%), then steadily increased leading up to the 2007 census (7.7 ± 7.0%). Prior to 1969, corn was primarily grown in eastern Kansas but modern increases have occurred predominantly in western Kansas (Figure S1). No state-level trends in the amount of land planted in agriculture were apparent from census data (Figure 1; Figure S2); however, there were regional shifts to lower proportion agriculture in eastern Kansas and increased agriculture in western Kansas in the early 1900s. The highest proportion of agricultural land occurred consistently in central Kansas. Farms were largest in western Kansas in all years and size increased steadily from 1910 (127.6 ± 77.4 ha) to 2007 (369 ± 195.6 ha; Figure 1; Figure S3).

3.2 | Population trends

Total spotted skunks harvested declined from 107,277 in 1928 to <200 in the 8 years preceding trapping season closure in 1978. Total striped skunks harvested also showed a decline from 279,647 in 1928, to 12,755 in 2010. Trapping effort was a significant predictor of harvest for both species (Table 1). We found no evidence that pelt price drove harvest of spotted skunk, but pelt price was a significant predictor harvest for striped skunks. Decreasing harvests were evident for both striped (pseudo-R^2 = 0.99) and spotted skunks (pseudo-R^2 = 0.99) after controlling for effort and pelt price (Figure 2). The period of greatest predicted decline occurred between 1928 and 1929, the earliest harvest data recorded for both species. Comparison of the 95% prediction intervals at the onset of trapping records suggested predicted corrected harvests for both species were comparable at the onset of trapping records, after which predicted spotted skunk harvests declined more rapidly than striped skunk harvests and declined to considerably lower harvests than those observed for striped skunks.

Declining harvests for spotted skunk were negatively correlated with the proportion of corn and farm size and appeared to coincide with large state-wide changes in these variables (Table 2). No correlation between spotted skunk harvest and agriculture was evident. For striped skunk, farm size was correlated with harvest but not corn or agriculture.

3.3 | Isotopic niche shifts

We sampled 90 striped and 89 spotted skunks collected between 1887 and 2012 from the FHSU teaching, MHP, KU, MVZ, USNM, TWTC and UMMZ collections (Figure S4). We identified six top models explaining the effect of landscape on δ^{13}C values (Table 3; Table S1). The variables species × corn, corn × farm size, species × average farm size and the quadratic effect of year were present in all top models. We found minimal support for the

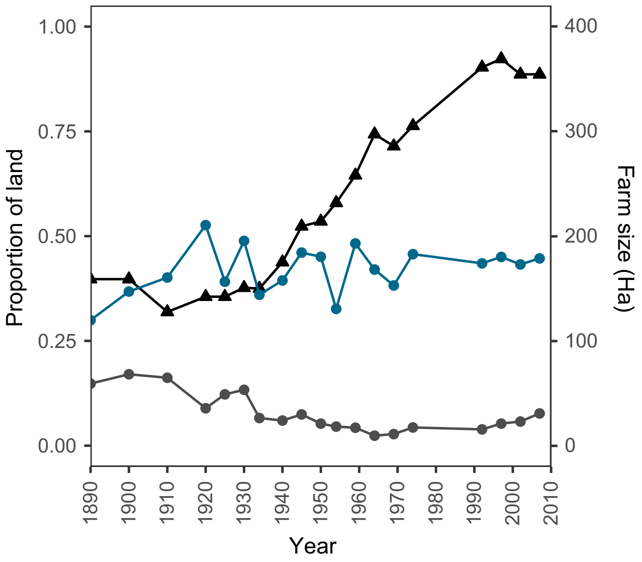


FIGURE 1 State mean farm size (pasture and agriculture; black triangles), proportion of total land area planted in corn (grey circles) and proportion of total land area in agriculture (blue circles) according to the United States Census of Agriculture 1890–2007

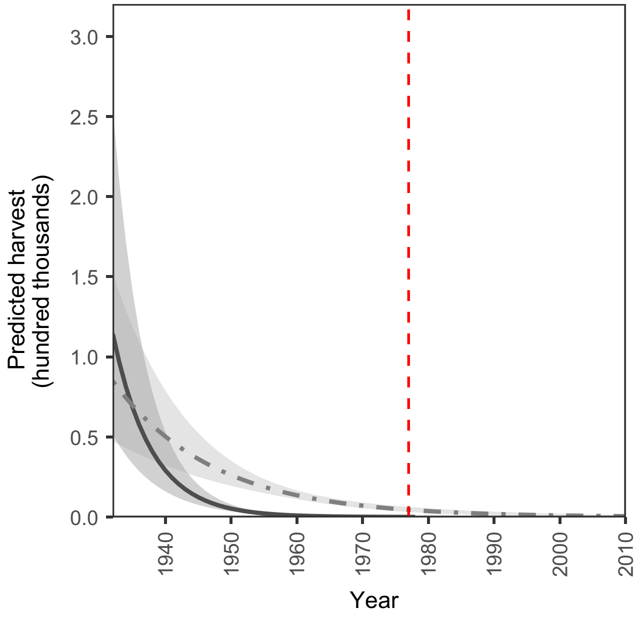


FIGURE 2 Predicted harvest and 95% prediction intervals for spotted skunk (solid, dark grey) and striped skunk (dot-dashed, light grey) in Kansas corrected for pelt price and trapping effort. The vertical dashed line marks the year (1978) trapping season for spotted skunk was closed

TABLE 1 Coefficients (*SE*s), *t* values and *p* values for models of spotted and striped skunk harvest. Data from Kansas, United States 1928–2010

	Spotted skunk			**Striped skunk**		
	Coefficient (*SE*)	***t* value**	***p***	**Coefficient (*SE*)**	***t* value**	***p***
Intercept	341.1 (28.03)	12.170	<0.001	135.7 (18.69)	7.261	<0.001
Year	−0.171 (0.014)	−11.950	<0.001	−0.065 (0.009)	−6.898	<0.001
Trap effort	0.000 (0.000)	3.450	0.000	0.000 (0.000)	7.259	<0.001
Pelt price	0.001 (0.023)	0.040	0.968	0.047 (0.02)	2.361	0.027

inclusion of agriculture, temperature and precipitation, which were each considered in only one top model. Model averaged predictions when all other covariates were held at their means indicated that spotted and striped skunk δ^{13}C values decreased between 1890 and 1933 (Figure 3a). After 1933, predicted δ^{13}C values stabilized for both species. Predicted spotted skunk δ^{13}C values were higher when corn was prevalent on the landscape; however, there was a slightly negative correlation between predicted δ^{13}C values and the proportion of corn planted for striped skunks (Figure 3b). For spotted skunk, higher predicted δ^{13}C values were associated with larger farms, while no trend was apparent for striped skunks (Figure 3c). When corn was prevalent on the landscape, predicted δ^{13}C values increased with farm size for both species (Figure 3d); however, widening prediction intervals suggested predictive ability was lost at values of farm size most common after 1950 (Figure S5).

Seven models were supported to describe the landscape level impacts on δ^{15}N values of spotted and striped skunks (Table 3; Table S2). There was considerable support for the effects species, corn and a quadratic effect of year, which were included in all top models, and some support for the effect of farm size which was included in six top models. We found minimal support for the inclusion of agriculture and temperature, which were considered in only 1 and 2 top models, respectively. Precipitation was not included in any top model. When all covariates were held at their means, model averaged predictions indicated spotted skunks had higher

TABLE 2 Correlations (rho and Bonferroni *corrected p* values presented) between predicted spotted (*Spilogale putorius*; $N = 10$) and striped skunk (*Mephitis mephitis*; $N = 14$) harvest and landscape variables proportion of total land area in active cropping (Agriculture), proportion of total land area planted in corn and farm size at the state level. Data from Kansas spotted skunks: 1925–1974 and striped skunks: 1920–2007

Species	Variable	rho	*p*
Spotted skunk	Agriculture	0.217	1.000
	Corn	0.902	<0.001
	Farm size	−0.984	<0.001
Striped skunk	Agriculture	0.103	1.000
	Corn	0.526	0.106
	Farm size	−0.967	<0.001

TABLE 3 Models assessing the influence of land use including farm size, proportion of total land area planted in corn and proportion of total land area in active cropping (Agriculture), species, year and temperature and precipitation on the δ^{13}C and δ^{15}N values of spotted and striped skunks in Kansas 1887–2012. All models with interactions contained main effects. Top models (i.e. $\Delta AIC_c < 2.0$) and the intercept-only null models are shown

	Model	K^a	Relative likelihood^b	$\Delta AIC_c{}^c$	w_i^d	Deviance	Adjusted R^2
δ^{13}C	Year^2 + Species × Corn + Farm Size × Corn + Farm Size × Species^e	10	1.000	0.00	0.117	733.079	0.269
	Year^2 + Species × Corn + Year × Species + Farm Size × Corn + Farm Size × Species	11	0.514	1.33	0.060	729.250	0.269
	Year^2 + Species × Corn + Farm Size × Corn + Farm Size × Species + Temperature	11	0.427	1.70	0.050	730.757	0.267
	Year^2 + Species × Corn + Species × Farm Size × Corn	11	0.405	1.81	0.047	731.209	0.267
	Year^2 + Species × Corn + Farm Size × Corn + Agriculture + Farm Size × Species	11	0.389	1.89	0.045	731.515	0.266
	Year^2 + Species × Corn + Farm Size × Corn + Precipitation + Farm Size × Species	11	0.345	2.13	0.040	732.482	0.265
	Null	2	0.000	47.10	0.000	1,050.21	
δ^{15}N	Year^2 + Species + Corn + Farm Size^e	7	1.000	0.00	0.053	386.136	0.280
	Year^2 + Species + Corn × Farm Size	8	0.687	0.75	0.037	384.992	0.282
	Year^2 + Species + Corn + Farm Size + Temperature	8	0.647	0.87	0.035	385.716	0.282
	Year^2 + Year × Species + Corn + Farm Size	8	0.436	1.66	0.023	394.691	0.278
	Year^2 + Species + Corn	6	0.415	1.76	0.022	385.589	0.269
	Year^2 + Species + Corn × Farm Size + Temperature	9	0.405	1.81	0.022	383.032	0.283
	Year^2 + Species + Corn + Farm Size + Agriculture	8	0.379	1.94	0.020	383.284	0.277
	Null	2	0.000	53.40	0.000	552.140	

[a] *K* is the number of parameters in the model.

[b] Relative Likelihood = $\exp(-0.5 \times \Delta AIC_c)$, the likelihood ratio of the given model to the top model.

[c] ΔAIC_c is the difference in the AIC_c between a given model and the top model.

[d] w_i is the AIC_c weights, or the probability that of the models tested the given model fits the data best.

[e] AIC_c of the top model = 781.7 (δ^{13}C) and 660.3 (δ^{15}N).

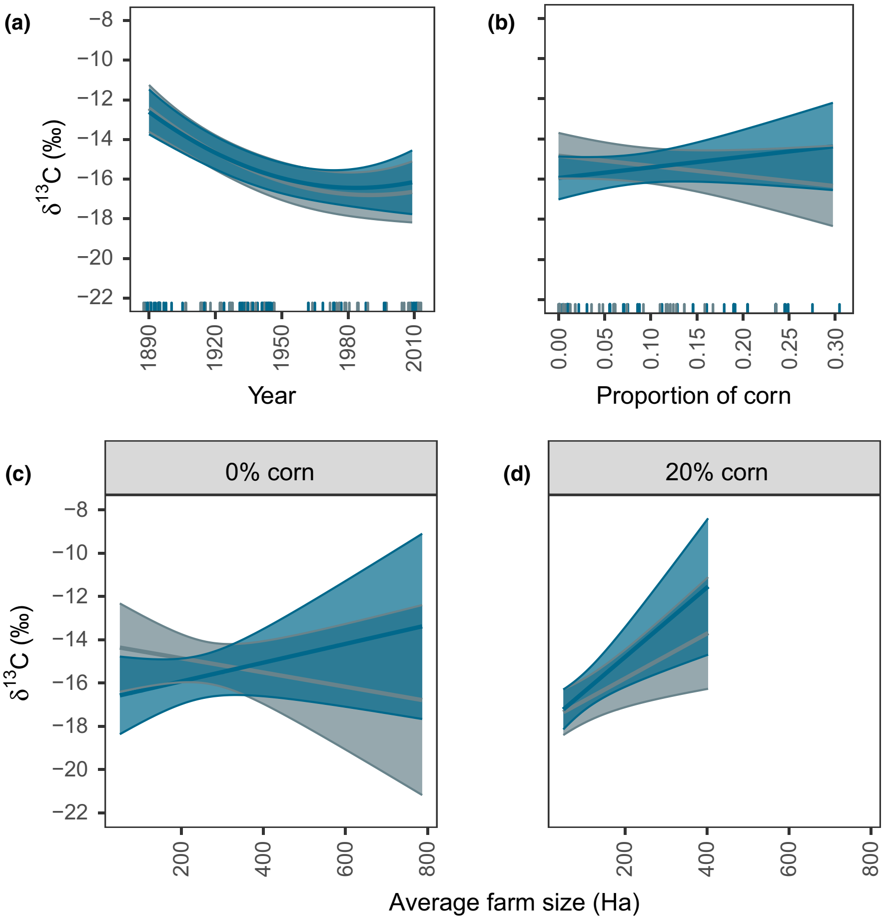


FIGURE 3 Model averaged predictions and 95% prediction intervals for the relationship between δ^{13}C values and (a) time, (b) the proportion of corn planted in the county, (c) average farm size at low prevalence of corn and d) average farm size at high prevalence of corn for spotted skunks (blue, dark) striped skunks (grey, light) when all other covariates are held at their mean values. Data collected from Kansas 1887–2012. Observed values for *x* variables of both species shown in rugs for plots (a) and (b)

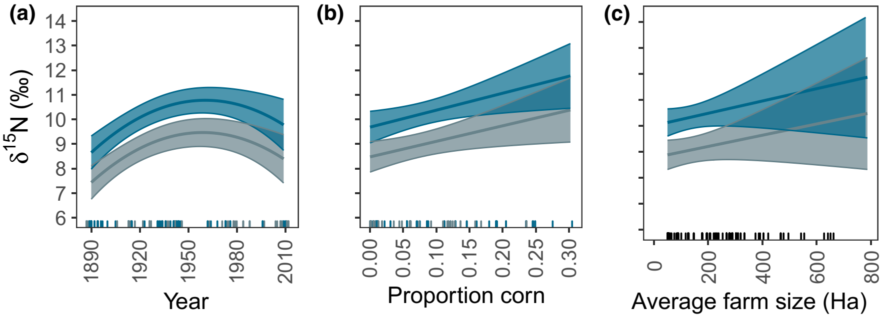


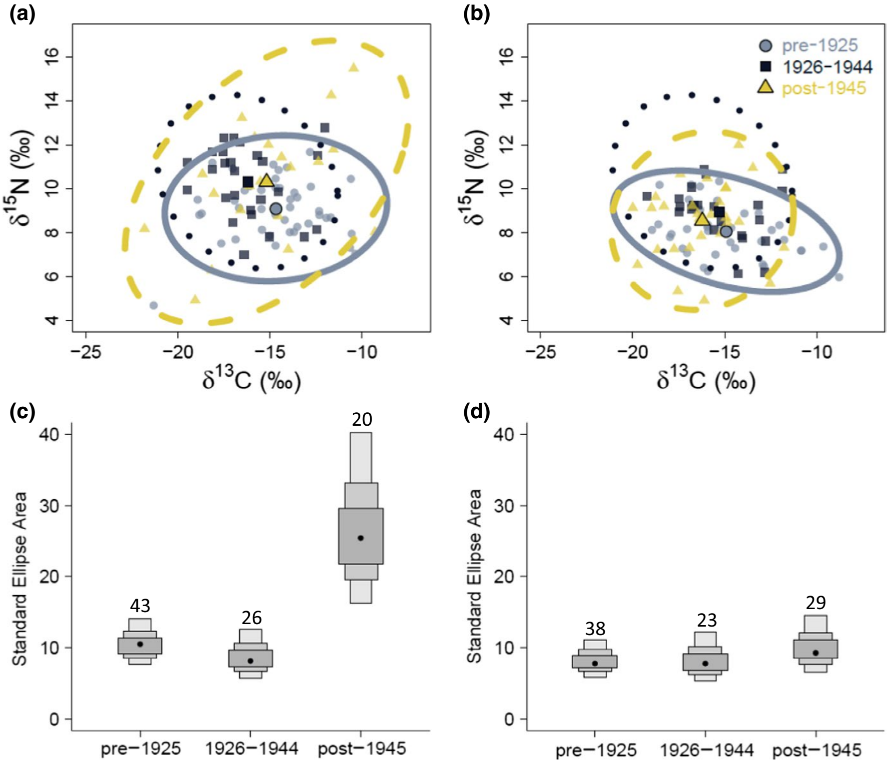
FIGURE 4 Model averaged predictions and 95% prediction intervals for the relationship between δ^{15}N values and (a) time, (b) the proportion of corn planted in the county and (c) average farm size, for spotted skunks (blue, dark) and striped skunks (grey, light) when all other covariates are held at their mean values. Data collected from Kansas 1887–2012. Observed values for *x* variables of both species shown in rugs

δ^{15}N values than striped skunks (Figure 4a). Predicted δ^{15}N values for both skunk species increased until 1960. After 1960, there was a trend towards lower δ^{15}N values for both species; however, predictive ability during this period was low as evidenced by widening 95% prediction intervals. Both spotted and striped skunk δ^{15}N values increased as the prevalence of corn increased from 0% to 30% of the landscape (Figure 3b) and with increasing farm size (Figure 4c), but widening prediction intervals suggested predictive ability was again lost at values of corn and farm size most common after 1950 (Figure S5).

3.4 | Isotopic niche breadth

The isotopic niche breadth for both spotted (Figure 5a) and striped skunks (Figure 5b) reflected alterations in both the axis of highest variation and eccentricity between pre- and during population declines compared to the post-decline bins. Following population decline, the mean isotopic niche breadth of spotted skunks increased from 10.8 (95% CI: 7.8, 14.1, *N* = 43) to 24.6 (95% CI: 14.6, 35.9, *N* = 20; Figure 5c). This expansion appeared to primarily result from increased use of diet items with divergent δ^{15}N

FIGURE 5 Orientation of the SIBER standard ellipsoids encapsulating the isotopic niche space and 95% CIs of (a) spotted skunk and (b) striped skunk pre-population decline, during decline, and post-population decline. The median Bayesian standard ellipse area and 95%, 75% and 50% CIs, quantifying niche space is also shown for (c) spotted skunk and (d) striped skunk during these periods. Data collected from Kansas 1887–2012. Numbers above CIs indicate sample size



values. Although mean isotopic niche breadth of striped skunks also increased slightly between pre-decline ($\bar{x} = 8.4$, 95% CI: 5.8, 11.3, $N = 38$) and post-decline periods ($\bar{x} = 10.8$, 95% CI: 7.1, 15.0, $N = 29$), we did not find a clear difference between the two groups (Figure 5d).

4 | DISCUSSION

Inferring the cause of historic declines in species is challenging, yet necessary for disentangling the primary drivers of population decline and determining appropriate conservation actions. Herein, we demonstrate that by coupling temporal isotopic niche reconstructions with land use and population data, it is possible to garner an increased understanding of the causes of past population declines. For Kansas spotted skunks, these methods highlight a transition from C_4-plant-based trophic systems and other basal trophic resources towards higher trophic level prey in a C_3-dominated system. Observed isotopic niche restructuring corresponded to the period of decline and dramatic land use changes across the state, supporting the hypothesis that the loss of a major and abundant basal resource (i.e. the C_4 plant corn) alongside land use changes, resulted in trophic network restructuring, isotopic niche expansion and subsequent population declines of spotted skunks.

Where ecosystems are highly dependent on a few key resources, a reduction in availability of these resources can lead to dramatic changes in ecosystem function and bottom-up trophic cascades (Hobart et al., 2019). Agriculture, in particular corn, has become a common food subsidy for wildlife including skunks (Crabb, 1941; Kelker, 1937; Selko, 1937) and a foundation of many trophic systems (Magioli et al., 2014; Boggie et al., 2018). Meanwhile, historically abundant natural prey such as insects have become less abundant as a result of increased use of pesticides and fertilizers (Sánchez-Bayo & Wyckhuys, 2019). For skunks, the reliance on corn kernels as a food source and corn-derived trophic systems likely increased throughout the 19th and 20th centuries as farm size increased and a combination of habitat loss to agriculture, reduced juxtaposition of agricultural and natural habitats, and the loss of other more natural prey sources created a novel baseline community structured around corn. Our data supported a historic reliance on C_4-based trophic systems by skunks. The modelled relationship between high $\delta^{13}C$ values and the abundance of corn on the landscape suggests that reduced reliance on C_4 systems is directly tied to the abundance of corn. Furthermore, this relationship suggested that reliance increased as a metric of agricultural intensification, farm size, increased possibly due to loss of alternative crops or other natural resources. Furthermore, predicted increases in $\delta^{15}N$ values suggested that both skunk species shifted towards consuming higher trophic level prey through the early 1900s, a trend that occurred to a greater degree in spotted skunks and was apparent when controlling for corn and farm size. Increased $\delta^{15}N$ values have been associated with expanded agricultural land use and a corresponding rise in fertilizer use; however, there was no support for variable $\delta^{15}N$ values by the amount of agricultural land in our study (Hebert & Wassenaar, 2001). Furthermore, while $\delta^{15}N$ values of different fertilizers are highly variable, organic fertilizers typically have higher $\delta^{15}N$ values than synthetic fertilizers (Bateman & Kelly, 2007). As a result, if changes in fertilizer use over time drove $\delta^{15}N$ values of skunks, $\delta^{15}N$ values should decrease over time as fertilizer use shifted from organic to synthetic fertilizers in the early-mid 1900s. However, we observed the opposite, suggesting temporal trends were indicative of a historical diet based on lower trophic levels. These trends towards lower δ^{15}N values suggest a historic reliance on corn kernels or a simplified trophic structure in prey species and subsequent shift to higher trophic level prey rather than a decrease resulting from changes in fertilizer use. High δ^{15}N values were also apparent as corn and as farm size increased; however, we lost predictive power for these trends at values that were observed most frequently after the early 1900s. We suggest that these trends might have been driven by early associations between skunks and use of fertilized agricultural land prior to the advent and widespread adoption of synthetic fertilizers. Alternatively, these trends could result from more complex trophic networks in these areas.

Changes in a population's niche space can result from altered resource availability or accessibility, due to factors such as novel interspecific interactions or alterations to the abiotic landscape (Scheele et al., 2017). For spotted skunks, the loss of a central dietary resource may have triggered a clear increase in the isotopic diversity of prey items taken. Declines in primary resources often result in increased dietary niche width for generalist foragers as alternative resources are increasingly incorporated (Korotkevich et al., 2018; Svanback & Persson, 2004; Wilson & Turelli, 1986). This trophic plasticity might allow individuals to incorporate novel resources, which can result in population growth and increased density; similarly, loss of high-quality resources can incur fitness consequences (Hobart et al., 2019). Skunk dietary isotopic niche space historically reflects behavioural specialization towards corn and corn-derived trophic systems, which were highly abundant in the late 1800s through the 1920s, and is supported by diet studies from this time (Crabb, 1941; Selko, 1937). Other authors have noted anecdotal reports that spotted skunks were rare or not present in the Great Plains prior to the proliferation of agriculture and hypothesized that the availability of agricultural subsidies, such as corn kernels, particularly during winter might have inflated populations above historic baselines and permitted range expansion (Choate et al., 1973). The later loss of corn as an abundant food resource likely resulted in increased reliance on alternative prey sources. As small vertebrates and invertebrates were commonly consumed in the absence of corn (Crabb, 1941; Selko, 1937), a general trend towards increased use of these higher trophic level prey where corn was less abundant would be expected. Notably, these resources also likely had a higher foraging cost than corn where corn was abundant, particularly as many prey species experienced concurrent declines, which could have resulted in lower spotted skunk survival and fecundity rates and subsequent population declines. Regardless of the initial drivers of population growth, our data suggested that the collapse of a historically important primary food source in this region, corn, resulted in niche restructuring and these changes were consistent with population declines of spotted skunks in the Great Plains.

While spotted skunks restructured their isotopic niche space in response to a reduction in corn plantings, there is no indication of population-scale isotopic niche expansion in striped skunks over similar spatiotemporal scales. Given that both skunks have similar ecologies as opportunistic generalists, this mismatch in niche dynamics over the past century further suggests that spotted skunk's increased dietary niche breadth was a result of reduction in corn-centric trophic networks rather than a shift in baseline δ^{13}C and δ^{15}N values over time. One potential reason why the reduction in corn had a disproportionate impact on spotted skunks is that there is a significant difference in body mass between the two mustelids, with striped skunks being on average 5 kg heavier than spotted skunks (Kinlaw, 1995; Wade-Smith & Verts, 1982). For mammalian carnivores, body mass is the leading factor for determining competitive dominance and is critical in dictating the metabolic needs of a species (Palomares & Caro, 1999). Being the larger of the two species, striped skunks would have been more likely to retain access to preferred resources, forcing competitively inferior spotted skunks to pursue other habitats and prey items as corn resources diminished. Furthermore, spotted skunks have higher metabolic needs than striped skunks during winter when striped skunks undertake seasonal torpor in underground dens while spotted skunks remain active. As such, spotted skunks may have had a heavier reliance on agricultural food subsidies to support populations during winter food scarcity than striped skunks making them more susceptible to negative impacts of their loss (Crabb, 1948; Wade-Smith & Verts, 1982). As litter sizes among skunks are highly variable, with delayed implantation and number of litters depending greatly on resource availability, the effects of competitive dominance and dietary resource exclusion combine to achieve profound impacts on population dynamics over time (Godin, 1982; Mead, 1968, 1981). Thus, spotted skunks are likely to be more susceptible to population declines under less optimal foraging conditions.

5 | CONCLUSIONS

Our results demonstrate the utility of combining reconstructions of historic isotopic niche space and land use data to infer the cause of enigmatic historic population declines. The availability of historic land use data and museum collections as a rich source of historic isotope data increasingly allow for backwards assessment of historical dietary niche dynamics in relation to landscape change. As such, we believe these techniques have broad applicability in identifying the causes of population declines in other taxa. For spotted skunks, correlations between land use data, isotopic niche and population declines suggest that historic changes to agricultural land use triggered a restructuring of the isotopic niche of spotted skunks to increase the variety in prey sources. This generalist dietary space was likely to be insufficient to support the energetic demands of spotted skunks while the potentially competitively dominant and metabolically buffered striped skunks remained relatively unaffected. Our results indicate that spotted skunk conservation efforts could be bolstered by management of trophic networks to increase the quality of food resources available to spotted skunk populations.

ACKNOWLEDGEMENTS

We thank B. Bott, B. Gaston, C. Curtis J. Oyster and M. Peak for assistance with data collection. Support was granted from the Kansas Department of Wildlife, Parks, and Tourism State Wildlife Grant (# T2-12-R-1) and the Kansas Academy of Science Student Research Grant.

AUTHORS' CONTRIBUTIONS

A.E.C. and E.J.F. conceived the ideas and designed the methodology; A.E.C. collected the data; A.E.C. and B.P.T. analysed the data; A.E.C. and B.P.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.tmpg4f4xq (Cheeseman et al., 2021).

ORCID

Amanda E. Cheeseman https://orcid.org/0000-0002-3744-0945
Brian P. Tanis https://orcid.org/0000-0001-9075-4057
Elmer J. Finck https://orcid.org/0000-0001-9289-4256

REFERENCES

Alisauskas, R. T., & Hobson, K. A. (1993). Determination of lesser snow goose diets and winter distribution using stable isotope analysis. *Journal of Wildlife Management*, *57*, 49–54. https://doi.org/10.2307/3808999

Ambrose, S. H. (1991). Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. *Journal of Archaeological Science*, *18*, 293–317. https://doi.org/10.1016/0305-4403(91)90067-Y

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, *74*, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Bateman, A. S., & Kelly, S. D. (2007). Fertilizer nitrogen isotope signatures. *Isotopes Environ Health Stud*, *43*, 237–247. https://doi.org/10.1080/10256010701550732

Boggie, M. A., Carleton, S. A., Collins, D. P., Vradenburg, J., & Sroka, C. J. (2018). Using stable isotopes to estimate reliance on agricultural food subsidies and migration timing for a migratory bird. *Ecosphere*, *9*, e02083. https://doi.org/10.1002/ecs2.2083

Bolker, B. M. (2008). *Ecological models and data in R*. Princeton University Press.

Brühl, C. A., Schmidt, T., Pieper, S., & Alscher, A. (2013). Terrestrial pesticide exposure of amphibians: An underestimated cause of global decline? *Scientific Reports*, *3*, 1135. https://doi.org/10.1038/srep01135

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach*. Springer.

Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, *96*, 2370–2382. https://doi.org/10.1890/14-1639.1

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*, e1400253. https://doi.org/10.1126/sciadv.1400253

Chamberlain, C. P., Waldbauer, J. R., Fox-Dobbs, K., Newsome, S. D., Koch, P. L., Smith, D. R., Church, M. E., Chamberlain, S. D., Sorenson, K. J., & Risebrough, R. (2005). Pleistocene to recent dietary shifts in California condors. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 16707–16711. https://doi.org/10.1073/pnas.0508529102

Chamberlain, S. (2019). *rnoaa: 'NOAA' weather data from R*. R package version 0.9.5. Retrieved from https://CRAN.R-project.org/package=rnoaa

Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. University of Chicago Press.

Chase, J. M., & Leibold, M. A. (2004). Ecological niches: linking classical and contemporary approaches. *Biodiversity & Conservation*, *13*, 1791–1793. https://doi.org/10.1023/B:BIOC.0000029366.24837.fc

Cheeseman, A. E., Tanis, B. P., & Finck, E. J. (2021). Data from: Quantifying temporal variation in dietary niche to reveal drivers of past population declines; stable isotope, harvest trends, and land use. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.tmpg4f4xq

Choate, J. R., Fleharty, E. D., & Little, R. J. (1973). Status of the spotted skunk, *Spilogale putorius*, in Kansas. *Transactions of the Kansas Academy of Science*, *76*, 226–233. https://doi.org/10.2307/3627104

Crabb, W. D. (1941). Food habits of the prairie spotted skunk in Southeastern Iowa. *Journal of Mammalogy*, *22*, 349–364. https://doi.org/10.2307/1374928

Crabb, W. D. (1948). The ecology and management of the prairie spotted skunk in Iowa. *Ecological Monographs*, *18*, 201–232. https://doi.org/10.2307/1948639

Cumming, G., & Finch, S. (2005). Inference by eye: Confidence intervals and how to read pictures of data. *American Psychologist*, *60*, 170–180. https://doi.org/10.1037/0003-066X.60.2.170

Czech, B., Krausman, P. R., & Devers, P. K. (2000). Economic associations among causes of species endangerment in the United States. *BioScience*, *50*, 593–601.

Diefendorf, A. F., Mueller, K. E., Wing, S. L., Koch, P. L., & Freeman, K. H. (2010). Global patterns in leaf ^{13}C discrimination and implications for studies of past and future climate. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 5738–5743. https://doi.org/10.1073/pnas.0910513107

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *268*, 25–29. https://doi.org/10.1098/rspb.2000.1325

English, P. A., Green, D. J., & Nocera, J. J. (2018). Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. *Frontiers in Ecology and Evolution*, *6*, 14. https://doi.org/10.3389/fevo.2018.00014

Feiner, Z. S., Rice, J. A., Bunch, A. J., & Aday, D. D. (2013). Trophic niche and diet overlap between invasive white perch and resident white bass in a southeastern reservoir. *Transactions of the American Fisheries Society*, *142*, 912–919. https://doi.org/10.1080/00028487.2013.788563

Fox, A. D., Elmberg, J., Tombre, I. M., & Hessel, R. (2017). Agriculture and herbivorous waterfowl: A review of the scientific basis for improved management. *Biological Reviews*, *92*, 854–877. https://doi.org/10.1111/brv.12258

Fox-Dobbs, K., Bump, J., Peterson, R., Fox, D., & Koch, P. (2007). Carnivore-specific stable isotope variables and variation in the foraging ecology of modern and ancient wolf populations: Case studies from Isle Royale, Minnesota, and La Brea. *Canadian Journal of Zoology*, *85*, 458–471. https://doi.org/10.1139/Z07-018

Gannes, L. Z., Del Rio, C. M., & Koch, P. (1998). Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *119*, 725–737. https://doi.org/10.1016/S1095-6433(98)01016-2

Godin, A. J. (1982). *Striped and hooded skunks. Wild mammals of North America: Biology, management, and economics*. J. A. Chapman & G. A. Feldhamer (Eds.), (pp. 674–687). The John Hopkins University Press.

Gompper, M. E., & Hackett, H. M. (2005). The long-term, range-wide decline of a once common carnivore: The eastern spotted skunk (*Spilogale putorius*). *Animal Conservation*, *8*, 195–201. https://doi.org/10.1017/S1367943005001964

Green, R. E., & Scharlemann, J. P. (2003). Egg and skin collections as a resource for long-term ecological studies. *Bulletin-British Ornithologists Club*, *123*, 165–176.

Guerrero, I., Morales, M. B., Oñate, J. J., Aavik, T., Bengtsson, J., Berendse, F., Clement, L. W., Dennis, C., Eggers, S., Emmerson, M., Fischer, C., Flohre, A., Geiger, F., Hawro, V., Inchausti, P., Kalamees, A., Kinks, R., Liira, J., Meléndez, L., … Weisser, W. W. (2011). Taxonomic and functional diversity of farmland bird communities across Europe: Effects of biogeography and agricultural intensification. *Biodiversity and Conservation*, *20*, 3663–3681. https://doi.org/10.1007/s10531-011-0156-3

Guzzo, M. M., Haffner, G. D., Legler, N. D., Rush, S. A., & Fisk, A. T. (2013). Fifty years later: Trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. *Biological Invasions*, *15*, 1695–1711. https://doi.org/10.1007/s10530-012-0401-z

Han, H., Wei, W., Hu, Y., Nie, Y., Ji, X., Yan, L. I., Zhang, Z., Shi, X., Zhu, L., Luo, Y., Chen, W., & Wei, F. (2019). Diet evolution and habitat contraction of Giant Pandas via stable isotope analysis. *Current Biology*, *29*, 664–669.e662. https://doi.org/10.1016/j.cub.2018.12.051

Hebert, C. E., & Wassenaar, L. I. (2001). Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in Western Canada. *Environmental Science & Technology*, *35*, 3482–3487. https://doi.org/10.1021/es001970p

Helgen, K., & Reid, F. (2016). *Mephitis mephitis*. The IUCN Red List of Threatened Species.

Hespanhol, L., Vallio, C. S., Costa, L. M., & Saragiotto, B. T. (2019). Understanding and interpreting confidence and credible intervals around effect estimates. *Brazilian Journal of Physical Therapy*, *23*, 290–301. https://doi.org/10.1016/j.bjpt.2018.12.006

Hobart, B. K., Jones, G. M., Roberts, K. N., Dotters, B. P., Whitmore, S. A., Berigan, W. J., Raphael, M. G., Keane, J. J., Gutiérrez, R., & Peery, M. Z. (2019). Trophic interactions mediate the response of predator populations to habitat change. *Biological Conservation*, *238*. https://doi.org/10.1016/j.biocon.2019.108217

Hobson, K. A., & Quirk, T. W. (2014). Effect of age and ration on diet-tissue isotopic (δ^{13}C, δ^{15}N) discrimination in striped skunks (*Mephitis mephitis*). *Isotopes in Environmental and Health Studies*, *50*, 300–306.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, M. C., Donohue, I., Jackson, A. L., Britton, J. R., Harper, D. M., & Grey, J. (2012). Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. *PLoS ONE*, *7*, e31757. https://doi.org/10.1371/journal.pone.0031757

Kagata, H., & Ohgushi, T. (2006). Bottom-up trophic cascades and material transfer in terrestrial food webs. *Ecological Research*, *21*, 26–34. https://doi.org/10.1007/s11284-005-0124-z

Keeling, C. D. (1979). The Suess effect: ^{13}Carbon-^{14}Carbon interrelations. *Environment International*, *2*, 229–300. https://doi.org/10.1016/0160-4120(79)90005-9

Kelker, G. H. (1937). Insect food of skunks. *Journal of Mammalogy*, *18*, 164–170. https://doi.org/10.2307/1374462

Kinlaw, A. (1995). *Spilogale putorius*. *Mammalian Species*, *511*, 1–7.

Koch, P. L., Fox-Dobbs, K., & Newsome, S. D. (2017). *The isotopic ecology of fossil vertebrates and conservation paleobiology*. The University of Chicago Press.

Korotkevich, A. Y., Potapov, A. M., Tiunov, A. V., & Kuznetsova, N. A. (2018). Collapse of trophic-niche structure in belowground communities under anthropogenic disturbance. *Ecosphere*, *9*, e02528. https://doi.org/10.1002/ecs2.2528

Landholt, L. M., & Genoways, H. H. (2000). Population trends in furbearers in Nebraska. *Transactions of the Nebraska Academy of Sciences*, *26*, 97–110.

Layman, C. A., Quattrochi, J. P., Peyer, C. M., & Allgeier, J. E. (2007). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters*, *10*, 937–944. https://doi.org/10.1111/j.1461-0248.2007.01087.x

Leopold, R. (2010). *Trends in Iowa wildlife populations and harvest 2009* (p. 248). Iowa Department of Natural Resources.

Lewthwaite, J. M., Debinski, D. M., & Kerr, J. T. (2017). High community turnover and dispersal limitation relative to rapid climate change. *Global Ecology and Biogeography*, *26*, 459–471. https://doi.org/10.1111/geb.12553

Magioli, M., Moreira, M. Z., Ferraz, K. M., Miotto, R. A., de Camargo, P. B., Rodrigues, M. G., da Silva Canhoto, M. C., & Setz, E. F. (2014). Stable isotope evidence of *Puma concolor* (Felidae) feeding patterns in agricultural landscapes in southeastern Brazil. *Biotropica*, *46*, 451–460.

Manlick, P. J., Petersen, S. M., Moriarty, K. M., & Pauli, J. N. (2019). Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations. *Functional Ecology*, *33*, 335–345. https://doi.org/10.1111/1365-2435.13266

Matson, S. D., Rook, L., Oms, O., & Fox, D. L. (2012). Carbon isotopic record of terrestrial ecosystems spanning the Late Miocene extinction of *Oreopithecus bambolii*, Baccinello Basin (Tuscany, Italy). *Journal of Human Evolution*, *63*, 127–139. https://doi.org/10.1016/j.jhevol.2012.04.004

Mazerolle, M. J. (2020). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3-1. Retrieved from https://cran.r-project.org/package=AICcmodavg

Mead, R. A. (1968). Reproduction in eastern forms of the Spotted skunk (genus Spilogale). *Journal of Zoology*, *156*, 119–136.

Mead, R. (1981). Delayed implantation in mustelids, with special emphasis on the spotted skunk. *Journal of Reproduction and Fertility. Supplement*, *29*, 11–24.

Mineau, P., & Whiteside, M. (2013). Pesticide acute toxicity is a better correlate of US grassland bird declines than agricultural intensification. *PLoS ONE*, *8*, e57457.

Muhly, T. B., Hebblewhite, M., Paton, D., Pitt, J. A., Boyce, M. S., & Musiani, M. (2013). Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. *PLoS ONE*, *8*, e64311. https://doi.org/10.1371/journal.pone.0064311

Murray, M., Cembrowski, A., Latham, A. D. M., Lukasik, V. M., Pruss, S., & St Clair, C. C. (2015). Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human–wildlife conflict. *Ecography*, *38*, 1235–1242. https://doi.org/10.1111/ecog.01128

Newsome, S. D., Etnier, M. A., Gifford-Gonzalez, D., Phillips, D. L., van Tuinen, M., Hadly, E. A., Costa, D. P., Kennett, D. J., Guilderson, T. P., & Koch, P. L. (2007). The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 9709–9714. https://doi.org/10.1073/pnas.0610986104

Newsome, S. D., Ralls, K., Van Horn Job, C., Fogel, M. L., & Cypher, B. L. (2010). Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). *Journal of Mammalogy*, *91*, 1313–1321. https://doi.org/10.1644/09-MAMM-A-362.1

Newsome, S. D., Yeakel, J. D., Wheatley, P. V., & Tinker, M. T. (2012). Tools for quantifying isotopic niche space and dietary variation at the individual and population level. *Journal of Mammalogy*, *93*, 329–341. https://doi.org/10.1644/11-MAMM-S-187.1

Nyhus, P. J. (2016). Human–wildlife conflict and coexistence. *Annual Review of Environment and Resources*, *41*, 143–171. https://doi.org/10.1146/annurev-environ-110615-085634

Olsson, K., Stenroth, P., Nystrom, P., & Graneli, W. (2009). Invasions and niche width: Does niche width of an introduced crayfish differ from a native crayfish? *Freshwater Biology*, *54*, 1731–1740. https://doi.org/10.1111/j.1365-2427.2009.02221.x

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, *153*, 492–508. https://doi.org/10.1086/303189

Papworth, S. K., Rist, J., Coad, L., & Milner-Gulland, E. J. (2009). Evidence for shifting baseline syndrome in conservation. *Conservation Letters*, *2*, 93–100. https://doi.org/10.1111/j.1755-263X.2009.00049.x

Peterson, A. T., Sánchez-Cordero, V., Martínez-Meyer, E., & Navarro-Sigüenza, A. G. (2006). Tracking population extirpations via melding ecological niche modeling with land-cover information. *Ecological Modelling*, *195*, 229–236. https://doi.org/10.1016/j.ecolmodel.2005.11.020

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ringelman, J. K. (1990). *13.4. 3. Managing agricultural foods for waterfowl. Waterfowl management handbook* (p. 23). United States Department of the Interior Fish and Wildlife Service.

Rossman, S., Ostrom, P. H., Gordon, F., & Zipkin, E. F. (2016). Beyond carbon and nitrogen: Guidelines for estimating three-dimensional isotopic niche space. *Ecology and Evolution*, *6*, 2405–2413. https://doi.org/10.1002/ece3.2013

Roth, J. D., & Hobson, K. A. (2000). Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: Implications for dietary reconstruction. *Canadian Journal of Zoology*, *78*, 848–852. https://doi.org/10.1139/z00-008

Sánchez-Bayo, F., & Wyckhuys, K. A. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, *232*, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Sasse, D. B., & Gompper, M. E. (2006). Geographic distribution and harvest dynamics of the eastern spotted skunk in Arkansas. *Journal of the Arkansas Academy of Science*, *60*, 119–124.

Scheele, B. C., Foster, C. N., Banks, S. C., & Lindenmayer, D. B. (2017). Niche contractions in declining species: Mechanisms and consequences. *Trends in Ecology & Evolution*, *32*, 346–355. https://doi.org/10.1016/j.tree.2017.02.013

Sedinger, J. S., & Alisauskas, R. T. (2014). Cross-seasonal effects and the dynamics of waterfowl populations. *Wildfowl*, 277–304.

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Selko, L. F. (1937). Food habits of Iowa skunks in the fall of 1936. *The Journal of Wildlife Management*, *1*, 70–76. https://doi.org/10.2307/3795763

Shaffer, H. B., Fisher, R. N., & Davidson, C. (1998). The role of natural history collections in documenting species declines. *Trends in Ecology & Evolution*, *13*, 27–30. https://doi.org/10.1016/S0169-5347(97)01177-4

Svanback, R., & Persson, L. (2004). Individual diet specialization, niche width and population dynamics: Implications for trophic polymorphisms. *Journal of Animal Ecology*, *73*, 973–982. https://doi.org/10.1111/j.0021-8790.2004.00868.x

Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., & Reist, J. D. (2015). A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology*, *96*, 318–324.

Szteren, D., Aurioles-Gamboa, D., Labrada-Martagón, V., Hernández-Camacho, C. J., & De María, M. (2018). Historical age-class diet changes in South American fur seals and sea lions in Uruguay. *Marine Biology*, *165*, 59. https://doi.org/10.1007/s00227-018-3315-1

Terry, R. C. (2018). Isotopic niche variation from the Holocene to today reveals minimal partitioning and individualistic dynamics among four sympatric desert mice. *Journal of Animal Ecology*, *87*, 173–186. https://doi.org/10.1111/1365-2656.12771

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*, 571–573. https://doi.org/10.1126/science.aaa4984

Urton, E. J., & Hobson, K. A. (2005). Intrapopulation variation in gray wolf isotope (δ^{15}N and δ^{13}C) profiles: Implications for the ecology of individuals. *Oecologia*, *145*, 316–325. https://doi.org/10.1007/s00442-005-0124-2

USFWS. (2012). Endangered and threatened wildlife and plants; 90-day finding on a petition to list the prairie gray fox, the plains spotted skunk, and a distinct population segment of the Mearn's eastern cottontail in east-central Illinois and western Indiana as endangered or threatened species. *Federal Register*, *77*, 71159–71771.

Wade-Smith, J., & Verts, B. J. (1982). *Mephitis mephitis*. *Mammalian Species*, *173*, 1–7. https://doi.org/10.2307/3503883

Wassenaar, L. I., & Hobson, K. A. (2000). Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. *Ecological Applications*, *10*, 911–916.

Wilson, D. S., & Turelli, M. (1986). Stable underdominance and the evolutionary invasion of empty niches. *The American Naturalist*, *127*, 835–850. https://doi.org/10.1086/284528

Yeakel, J. D., Guimarães, P. R. Jr, Bocherens, H., & Koch, P. L. (2013). The impact of climate change on the structure of Pleistocene food webs across the mammoth steppe. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20130239. https://doi.org/10.1098/rspb.2013.0239

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Cheeseman AE, Tanis BP, Finck EJ. Quantifying temporal variation in dietary niche to reveal drivers of past population declines. *Funct Ecol*. 2021;35:930–941. https://doi.org/10.1111/1365-2435.13765