



Research Article

Effects on White-Tailed Deer Following Eastern Coyote Colonization

EUGENIA V. BRAGINA,¹ *Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA*

ROLAND KAYS, *North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, NC 27601, USA*

ALLISON HODY, *Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA*

CHRISTOPHER E. MOORMAN, *Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA*

CHRISTOPHER S. DePERNO, *Fisheries, Wildlife, and Conservation Biology Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA*

L. SCOTT MILLS, *Wildlife Biology Program and Office of Research and Creative Scholarship, University of Montana, Missoula, MT 59812, USA*

ABSTRACT The expansion or recovery of predators can affect local prey populations. Since the 1940s, coyotes (*Canis latrans*) have expanded into eastern North America where they are now the largest predator and prey on white-tailed deer (*Odocoileus virginianus*). However, their effect on deer populations remains controversial. We tested the hypothesis that coyotes, as a novel predator, would affect deer population dynamics across large spatial scales, and the strongest effects would occur after a time lag following initial coyote colonization that allows for the predator populations to grow. We evaluated deer population trends from 1981 to 2014 in 384 counties of 6 eastern states in the United States with linear mixed models. We included deer harvest data as a proxy for deer relative abundance, years since coyote arrival in a county as a proxy of coyote abundance, and landscape and climate covariates to account for environmental effects. Overall, deer populations in all states experienced positive population growth following coyote arrival. Time since coyote arrival was not a significant predictor in any deer population models and our results indicate that coyotes are not controlling deer populations at a large spatial scale in eastern North America. © 2019 The Wildlife Society.

KEY WORDS eastern coyote, novel predator, population growth rate, predator-prey dynamics, spatial compensation.

Predators can affect prey population dynamics and initiate cascading effects throughout the ecosystem, especially when the predator is invasive or recolonizing (Levi and Wilmers 2012, Newsome and Ripple 2015, Wallach et al. 2015). The effect of predation on prey dynamics at a landscape level depends on predator and prey behaviors and demographic responses (Holling 1959). Also, effects on prey population dynamics are tempered by whether predation has additive effects on mortality or is compensated for by changes in population vital rates (Patterson and Messier 2003, Hurley et al. 2011), and by the reproductive value of the age classes killed (Robinson et al. 2014). Collectively, these factors complicate the effects that a novel predator may have on population growth and persistence of native prey species (Mills 2013). As a result, predation may lead to a significant

decline of prey abundance (Hudgens and Garcelon 2011), no effect, or variable effects on prey abundance over time.

The expansion of coyotes (*Canis latrans*) over the last 65 years from their historical range in the arid open country of mid-west North America into the forests of eastern North America (Fener et al. 2005, Levy 2012; Fig. 1) offers a large-scale natural experiment to evaluate the effect of predator on prey. Eastern coyotes (*Canis latrans* var.) are capable of affecting smaller predators and prey species (Levi et al. 2012, Newsome and Ripple 2015), but their influence on white-tailed deer (*Odocoileus virginianus*) populations remains controversial. White-tailed deer fawn mortality from coyotes can reach 80% of all mortalities (Vreeland et al. 2004; Kilgo et al. 2012; Chitwood et al. 2015a, b). Also, coyotes kill adult deer but do not typically hunt in packs, and their effectiveness as predators of adults remains in question (Messier et al. 1986, Chitwood et al. 2014).

Local studies provide contradictory evidence as to the extent to which coyotes are affecting deer abundance and population growth rate in the eastern United States. Fawn survival in the presence of coyotes can be low, causing local

Received: 9 December 2017; Accepted: 11 January 2019

¹E-mail: e.bragina@gmail.com

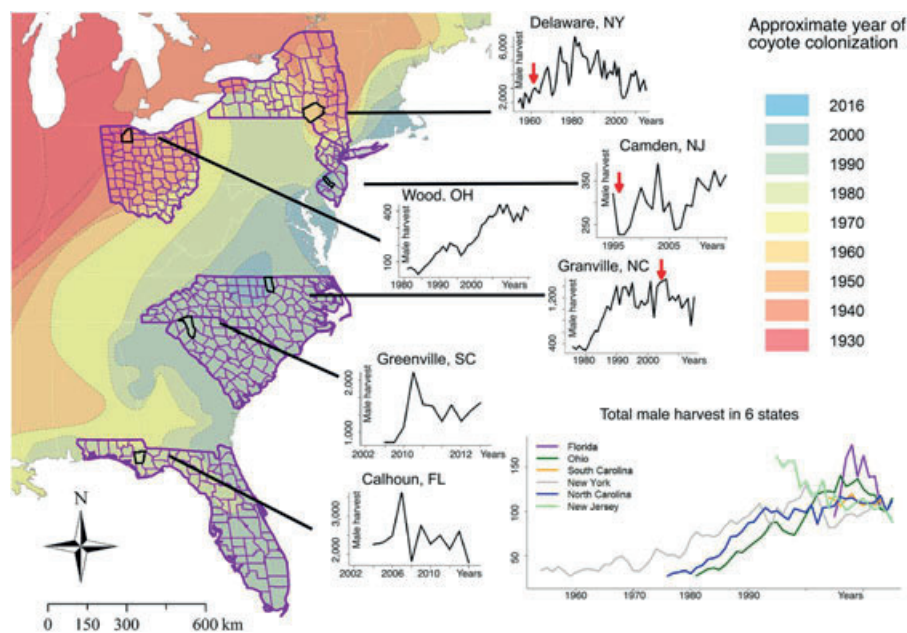


Figure 1. Coyote colonization and white-tailed deer harvest in 1930–2016 (Hody and Kays 2018). In each of 6 states, we plotted male deer harvest in a randomly chosen county as an example. Red arrows in Delaware, New York; Camden, New Jersey; and Granville, North Carolina, show the time of coyote arrival. In Wood, Ohio; Greenville, South Carolina; and Calhoun, Florida, coyote arrived before the first deer harvest data were available. Bottom right inset shows male deer harvest in each state.

population declines (Chitwood et al. 2015a, b), and coyote-caused mortality is thought to be additive rather than compensatory (Patterson and Messier 2003). Indeed, some coyote removal experiments in the eastern United States have shown deer recruitment increases 2–3 times following coyote removal (Howze et al. 2009, VanGilder et al. 2009, Kilgo et al. 2014). However, other removal experiments had little or no effect on deer populations, especially several years after removal was stopped (Brown and Conover 2011, Hurley et al. 2011, Gulsby et al. 2015). The restricted temporal and spatial scopes of these previous studies have limited their ability to determine the overall effects of coyotes on deer in the eastern United States.

Furthermore, the response of prey to a novel predator is expected to change over time (Hayes et al. 2006, Schreiber and Vejdani 2006, Fisk et al. 2007). This theory leads to a prediction that when coyotes first arrive in a county, they would not be abundant enough to affect deer population growth rate. However, after coyotes become more abundant, deer population growth rate may decline because of predator numerical and functional responses. Effects of predators on prey numbers regionally can be diluted by spatial compensation across the landscape, whereby population-specific harvest rates are compensated for by movement of individuals into the harvested populations (Harveson et al. 2004, Novaro et al. 2005, Newby et al. 2013). Because spatial compensation is likely to be missed by small-scale studies of single populations, an evaluation of deer population dynamics across a heterogeneous landscape requires larger-scale analysis across space and time.

Other covariates associated with land use cover, climate, and human effects may affect deer population dynamics separate from or in combination with coyote predation. For

example, coyote predation on deer fawns is less likely when land use cover is heterogeneous (i.e., fawns with more fragmented habitat in their home range are more likely to avoid coyote predation; Gulsby et al. 2017). Likewise, land use cover can affect eastern coyote density, with higher densities in more open forest and early-succession plant communities (e.g., grassland) compared to closed-canopy, mature forest (Kays et al. 2008). Climate mediates predation on white-tailed deer (Nelson and Mech 1986) and coyote density (Kays et al. 2008) and interacts with land cover (Ozoga and Gysel 1972). Finally, because human presence might mediate predator-prey interaction (Hebblewhite et al. 2005), we considered human density an important covariate when modeling relationships between coyotes and deer populations.

We assessed white-tailed deer population dynamics following coyote arrival in 6 eastern states of the United States. Specifically, we tested how deer population growth rate changed following coyote colonization, accounting for other environmental covariates that may mediate the effects of coyotes on deer population growth. If coyotes are affecting deer, we expected that deer population growth rate would decline following coyote colonization.

STUDY AREA

We conducted the analysis at the county level with 384 counties (531,312 km²) across 6 states (FL, NJ, NY, NC, OH, SC). The study period spanned 1981–2014. The region has numerous climatic zones, including humid continental, temperate, sub-tropical, tropical, and arid. Elevation ranges from seaboard level to the Appalachian Mountains. The summer months are warm, with length of summer, frost free season, and snowfall greatly varying from north to south

(NOAA Online Weather Data [NOWData], <http://w2.weather.gov/climate/xmacis.php?wfo=btv>, accessed 12 Dec 2016). Forests cover 34.4% of the study area, and deciduous trees dominate (22.2%). The northern portion of the study area is more forested (45.5% in NY) than the southern portion (19.4% in FL). Crop covers 29.4% of the area (U.S. Geological Survey [USGS] National Land Cover Dataset). In addition to white-tailed deer and coyotes, the mammal fauna includes American black bear (*Ursus americanus*), red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), and beaver (*Castor canadensis*; Whitaker and Hamilton 1998).

METHODS

We used time series of white-tailed deer harvest data from state wildlife agencies as proxies for regional deer abundance over time; directly estimated deer abundance does not exist across the long-term, regional spatial scale of our study. Deer harvest data have limitations in tracking true abundance (Weinstein 1977, Winterhalder 1980, Lambin et al. 1999). Widespread harvest data, however, can successfully index relative changes in ungulate abundance over time and space (Cattadori et al. 2003, Imperio et al. 2010).

Therefore, we indexed deer population growth (λ) over n years from initial time t as:

$$\lambda = \sqrt[n]{\text{harvest}(t+n)/\text{harvest}(t)} \quad (\text{Eq. 1})$$

We conducted analysis on deer harvest and male-only harvest. Florida Fish and Wildlife Conservation Commission provided data for 2005–2014, New Jersey Department of Environmental Protection for 1996–2016, New York Department of Environmental Conservation for 1954–2015, North Carolina Wildlife Resource Commission for 1981–2015, Ohio Department of Natural Resources for 1981–2015, and South Carolina Department of Natural Resources for 2004–2014. Management regulations implemented by state agencies changed throughout the timing of our study (1981–2016; Table 1).

Likewise, our analysis would ideally include rigorous field estimates of local coyote distribution and abundance across the 531,312-km² study area for the past 35 years. The only available data across eastern states, however, are numbers of coyotes harvested by trappers. Although these data do show rapid increases in trapper success following coyote colonization (Fig. 2), trapping data are unsuitable as a covariate in our statistical analysis for several reasons including erratic and locally variable monitoring protocols and small sample sizes. Therefore, we used length of time since colonization in a county as the covariate to index the expected effect of coyotes on deer population growth. The length of time since colonization is strongly associated with increased abundance and distribution for generalist introduced species such as coyotes (Crooks and Soulé 1999, Levy 2012). The first verified coyote sighting in Florida was in the 1960s (Main et al. 2000), the mid-1950s in New Jersey (New Jersey Division of Fish and Wildlife, unpublished data), 1925 in New York (Severinghaus 1974 cited by Fener et al. 2005), the 1970s in North Carolina (North Carolina Wildlife Resource Commission, unpublished data), 1919 in Ohio

(Weeks et al. 1990), and 1979 in South Carolina (South Carolina Department of Natural Resources, unpublished data).

To describe the timing of coyote colonization, we also mapped approximate coyote distribution in 1930–2016 based on georeferenced museum specimens, local reports of coyote colonization by state agencies, and peer-reviewed publications. We acquired the museum records from VertNet (vertnet.org, accessed 15 Jun 2016), a collaborative biodiversity database that catalogues data from hundreds of museum collections (Appendix 1, available online in Supporting Information). We queried the database for records associated with the preserved remains of coyotes and coyote hybrids (*C. latrans* × *rufus*, *C. latrans* × *familiaris*) collected between 1850 and 2016 at a known location, specified by either georeferenced coordinates or a county-state location. We grouped all available occurrence data by decade to approximate coyote colonization in each period. We identified the probable range of coyotes as of 1930 by forming a bounding polygon around VertNet locations from 1850–1930. We repeated the process with data from each additional decade to approximate the regional distribution of coyotes in each period. We used the contours of this map to derive county-level estimates of the number of years since coyote colonization.

Because our map of coyote colonization might incur errors based on factors such as museum funding and curator efforts, we conducted all analyses with a measure of coyote colonization derived from raw records of coyote colonization from the state agencies and related publications (Weeks et al. 1990, Main et al. 2000, Fener et al. 2005; agency data). The results did not differ from the models with coyote arrival estimated from museum records (unpublished analyses available on request).

To account for time lags in deer average annual population growth rate, we estimated λ (Eq. 1) across 7 periods from 1981 to 2014. Constraints in data availability for deer harvest and coyote colonization at the county level necessitated the use of categories of years spanning 3- to 5-year periods: population growth rate in 1981–1985, 1985–1990, 1990–1995, 1996–2000, 2000–2005, 2005–2010, and 2011–2014. Because 1 value of population growth takes at least 2 years to calculate (Eq. 1), we used years 1985, 1990, 2000, 2005, and 2010 for previous and following periods. For each period, we scaled the deer population growth index (λ) to an annual rate.

We incorporated the environmental covariates associated with land use, climate, and human densities in the model as direct and interactive effects. For climate and land use cover, we extracted the average value of each environmental covariate for each county. We used several climate covariates from the Bioclim dataset (Hijmans et al. 2005): BIO5 (max. temp of warmest month; all temperature variables were in C°), BIO6 (min temp of coldest month), BIO7 (temp annual range [BIO5 – BIO6]), BIO12 (annual precipitation), BIO15 (precipitation seasonality [CV]), BIO17 (precipitation of driest quarter), and altitude. We used snow cover duration obtained from the German Aerospace Center (German Remote Sensing Data Center, www.DLR.de/

Table 1. White-tailed deer harvest estimation methods and changes in management regulations (1981–2014) in 6 states in the eastern United States.

Deer harvest estimation methodology		Most important deer management regulation changes	
		Total harvest	Male harvest
Ohio Department of Natural Resources (C. McCoy, personal communication)	Harvest reporting is mandatory and the estimates are a minimum count of reported harvests (i.e., estimates do not account for harvested but not reported deer).	Most of changes aimed for more opportunities for hunters (e.g., in 1984, 24 out of 88 counties changed males-only to either-sex season; in 2007, 38 out of 88 counties changed bag limit from 3 to 6 deer).	Remains the same.
New York Department of Environmental Conservation (Batcheller and Rixinger 2011)	Harvest reporting is mandatory. About 15,000 killed deer are encountered in the field (exact number is stratified by wildlife management units) and percent of those reported is estimated and used as a true report rate to adjust number of reported kills similarly to Lincoln-Petersen index.	Most of changes aimed for more opportunities for hunters (e.g., authority to issue ≥ 1 deer management permit to an individual [1991], a prohibition on feeding wild deer [2002]).	Mostly remains the same, with minor exceptions (e.g., all deer management permits restricted to antlerless deer only [1993], antler restriction [3 points on 1 side], pilot study in 4 out of 92 wildlife management units [2005, 2006]).
New Jersey Department of Environmental Protection (C. Stanko, personal communication)	Harvest reporting is mandatory. Changed from live check stations to electronic deer check in 2012.	Most changes expanded opportunity for the take of antlerless deer, either by season expansion or increase in bag limit. In 1999, an Earn A Buck requirement was added to all seasons in certain zones. This has been slowly removed as deer densities were lowered in huntable areas.	1995–1998: hunters could harvest multiple males within the defined bag limit and permit season quotas. 1999–2001: hunters were restricted to 1 male/season and 2/6-day firearm season (i.e., max. of 7 males/hunter). 2002–present: hunters are restricted to 1 male/season and 2/6-day firearms season. If they take 2 during the 6-day, however, they forfeit the Permit Shotgun season male so the maximum is 6 males/hunter/deer year.
North Carolina Wildlife Resource Commission (Myers 2013)	Mail survey to randomly selected approximately 4% of licensed hunters. A modified tailored design method (Dillman 2011) with 3 mailings was used to evaluate for potential non-response bias. Response rate yields about 44.4% over the 3 mailings.	Most of changes aimed for more opportunities for hunters, e.g., daily bag limit increased to 2 deer in 3 out of 4 seasons (1984); state-wide bag limit changed to daily-2, possession-5, and season-5, of which 1 must be antlerless (1992) to daily-2, possession-6, and season-6, of which 2 must be antlerless (1997) and to daily-2, possession-6, and season-6, of which 4 must be antlerless (2000); daily bag limit removed (2010).	
South Carolina Department of Natural Resources (Ruth and Cantrell 2016)	Mail survey to randomly selected approximately 20% Big Game Permit holders of all license types. Response rate yields about 20%, which results in approximately 4% percent sampling rate on the entire licensee population.	In response to declining trend, the maximum number of either sex days was 21 in 2004, reduced to 16 or 17 depending on the calendar between 2004 and 2007, 12 between 2008 and 2012, and 8 in 2014. The antlerless deer bag limit on either sex days was reduced from 2 to 1 in 2014. Since 2004, number of antlerless tags issued through Deer Management Assistance Program has been decreased by approximately 20%.	Remains the same.
Florida Fish and Wildlife Conservation Commission (C. Morea, personal communication)	Before 2012: random mail survey to approximately 20% of all type permit holders. Response rate yields about 6–7%, which results in approximately 1.5% percent sampling rate on the entire licensee population. Since 2012: 2-phases telephone survey of deer hunters. The sample of hunters consisted of any deer license type. In the first phase, a random not-stratified sample of all Florida deer hunters was surveyed. This initial survey showed proportion of hunters in each Deer Management Unit, and a sample for the second survey was stratified accordingly (Florida Fish and Wildlife Conservation Commission).	Remain the same.	Since 2014, all antlered deer must have at least 2 or 3 points (depending on deer management unit) on 1 side or have a main beam length of 25.4 cm or more to be legal to take.

eoc, accessed 03 Sep 2016; Dietz et al. 2015); these estimates were based on the normalized difference snow index (NDSI), which is derived from radiance data acquired by the moderate resolution imaging spectroradiometer (MODIS). For land use cover covariates, we used the USGS National Land Cover Datasets (http://www.mrlc.gov/nlcd11_data.php, accessed 11 Sep 2016) available for 1992, 2001, 2006, and 2011. We extracted data from all 4 datasets and calculated Pearson correlation coefficients

between the same land cover classes for different years (e.g., correlation between percent of a county area covered with deciduous forest in 2001 and 2011). Correlation coefficients between the same land use classes in different years were always ≥ 0.8 ; therefore, we chose to use land cover data for the year of 2011 as the most recent and precise. We calculated percent of a county area covered with 1) water, 2) low-intensity developed (impervious area $< 50\%$), 3) high-intensity developed (impervi-

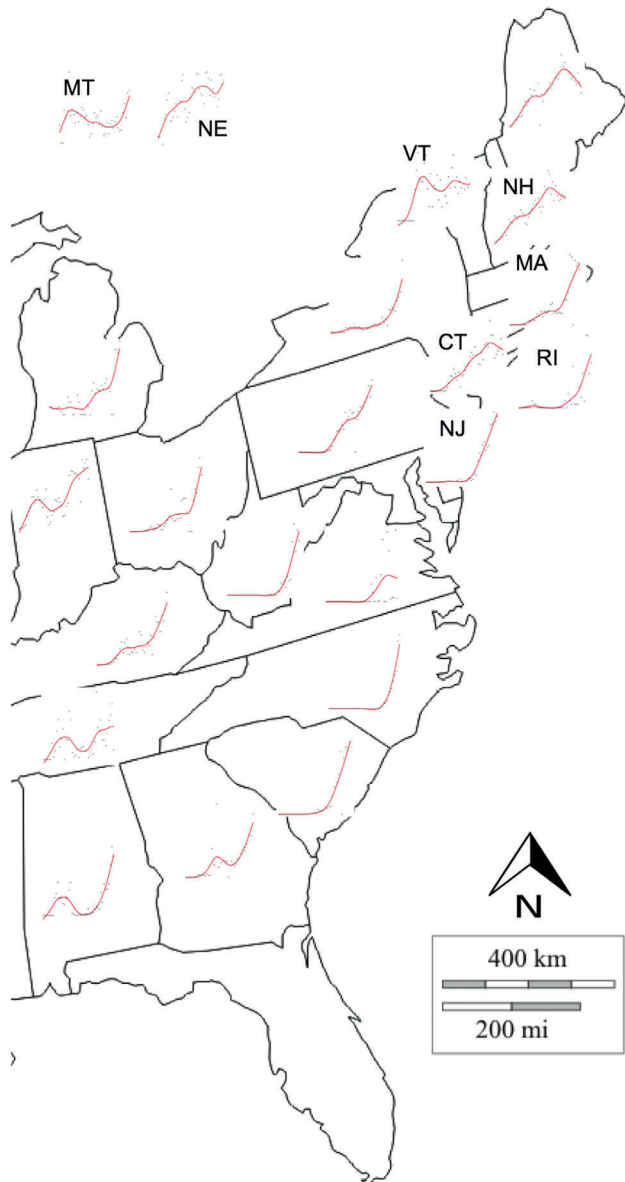


Figure 2. Coyotes harvested by trappers in 20 eastern United States from 1970 to 2015 showing a consistent increase across the region. We include 2 examples of western states for comparison. The red lines highlight smoothed relationship through annual harvest numbers (black dots). Scale of y-axis varies across states. Data for Maryland, Delaware, and Florida were incomplete and are not shown (U.S. Furbearer Conservation Technical Working Group of the Association of Fish and Wildlife Agencies, unpublished data).

ous area $\geq 50\%$), 4) deciduous forest, 5) mixed forest, 6) evergreen forest, 7) shrub, 8) grassland and pasture together, 9) crops, 10) woody wetlands, 11) herbaceous wetlands, and 12) average area covered with tree canopy as a proxy for canopy openness, which affects predation rate of coyotes on fawns (Gulsby et al. 2017). Also, we acquired data on net primary productivity from the National Aeronautics and Space Administration (NASA) Earth Observations (http://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD17A2_M_PSN, accessed 04 Oct 2016) to reflect amount of early successional vegetation, and calculated median and standard deviation of annual net primary productivity for each county. For a human density covariate at the county level, we acquired data from the United States Census Bureau for every 5-

year period (i.e., 1980, 1985, 1990, ...), but because the data over time were highly correlated ($r \geq 0.94$), we used only 2010 data.

After correlation analysis, we excluded variables with a correlation coefficient > 0.6 (Dormann et al. 2013), settling on 11 covariates to include in the deer-coyote population model: 1) number of years since coyote arrival, 2) average duration of snow pack in a county (number of days an area covered with snow), 3) human population density, 4) BIO12 (annual precipitation), 5) BIO15 (precipitation seasonality [CV]), 6) BIO17 (precipitation of driest quarter), 7) percent of county area covered with mixed forest and 8) low-intensity developed area, 9) average tree canopy openness, and 10) median and 11) standard deviation of annual net primary productivity (NPP) for each county.

The analysis included 2 groups of models: deer population growth rate based on male harvest, and deer population growth rate based on total harvest. Each group included 7 analyses because we fit the same model for each time period (i.e., 1981–1985, 1985–1990, ...); we fit 14 models. We fit a linear mixed model with a state as a random effect, and number of years since coyote arrival and 10 other covariates as fixed effects. Also, we expected that interactions between number of years since coyote arrival and habitat covariates would be important because of coyote habitat use and included interactions of number of years since coyote arrival with all other covariates. Deer population growth rate was the response variable in all models. Comparison of models with independent and correlated residuals showed that spatial autocorrelation substantially improved models according to Akaike's Information Criterion (AIC) weight (Tables 2 and 3), so we fit models with exponential correlation of residuals (Zuur et al. 2009):

$$1. \ln(\lambda_{\text{male/total}})_{ij} = \beta_0 + \beta_1 \text{coyote}_{ij} + \beta_2 \text{snow cover}_{ij} + \beta_3 \text{human population}_{ij} + \beta_4 \text{BIO12}_{ij} + \beta_5 \text{BIO15}_{ij} + \beta_6 \text{BIO17}_{ij} + \beta_7 \text{mixed forest}_{ij} + \beta_8 \text{developed area}_{ij} + \beta_9 \text{tree canopy}_{ij} + \beta_{10} \text{median(NPP)}_{ij} + \beta_{11} \text{SD(NPP)}_{ij} + \beta_{12} \text{coyote}_{ij} \times \text{snow cover}_{ij} + \beta_{13} \text{coyote}_{ij} \times \text{human population}_{ij} + \beta_{14} \text{coyote}_{ij} \times \text{BIO12}_{ij} + \beta_{15} \text{coyote}_{ij} \times \text{BIO15}_{ij} + \beta_{16} \text{coyote}_{ij} \times \text{BIO17}_{ij} + \beta_{17} \text{coyote}_{ij} \times \text{mixed forest}_{ij} + \beta_{18} \text{coyote}_{ij} \times \text{developed area}_{ij} + \beta_{19} \text{coyote}_{ij} \times \text{tree canopy}_{ij} + \beta_{20} \text{coyote}_{ij} \times \text{median(NPP)}_{ij} + \beta_{21} \text{coyote}_{ij} \times \text{SD(NPP)}_{ij} + u_j + \varepsilon_{ij}$$

where $\ln(\lambda_{\text{male/total}})$ is natural log-transformed deer population growth rate in county i in state j calculated with either male or total harvest for each time period,

$u_j \sim N(0, d^2)$ is intercept of a random effect(state), and

$$\varepsilon \sim N(0, \sigma^2)$$

$$\text{cor}(\varepsilon_s, \varepsilon_t) = \begin{cases} 1 & \text{if } s = t \\ b(\varepsilon_s, \varepsilon_t, \rho) & \text{else} \end{cases}$$

where b is a correlation function of parameter ρ describing correlation between residuals of the model, and s and t are 2 random counties (Zuur et al. 2009).

Table 2. Relationship between eastern coyote colonization and white-tailed deer male harvest in 6 states in the eastern United States, 1981–2014. We present Akaike’s Information Criterion (AIC) values for the full models with and without spatial correlation and best models, model weights (w_i), and the number of parameters (K). The best model for every period was the one without covariates.

Period	Full model ^a , no spatial correlation				Full model with spatial correlation				The best model ^b		
	AIC	ΔAIC	w_i	K	AIC	ΔAIC	w_i	K	AIC	w_i	K
1981–1985	−74.0	381.4	0.00	14	−108.2	347.2	0.00	15	−455.4	1	4
1985–1990	−223.6	326.2	0.00	14	−222.9	326.9	0.00	15	−549.8	1	4
1990–1995	−286.3	385.9	0.00	14	−304.7	367.5	0.00	15	−672.2	1	4
1996–2000	−372.1	393.3	0.00	14	−380.8	384.6	0.00	15	−765.4	1	4
2000–2005	−418.3	363.5	0.00	14	−416.3	365.5	0.00	15	−781.8	1	4
2005–2010	−322.3	351.8	0.00	14	−339.1	335.0	0.00	15	−674.1	1	4
2011–2014	−100.9	470.8	0.00	14	−213.6	358.1	0.00	15	−571.7	1	4

^a The full model included state as a random effect and the covariates years since coyote arrival, average duration of snow pack, human population density, annual precipitation, precipitation seasonality, precipitation of driest quarter, mixed forest cover, low-intensity developed area, average tree canopy openness, and median and standard deviation of annual net primary productivity.

^b The highest-ranked model included the intercept, spatial autocorrelation structure, and a random effect of state.

We chose the highest-ranked model according to the lowest AIC value (Burnham and Anderson 2002). We conducted all analysis using R statistical software version 3.3.1, packages nlme (Pinheiro et al. 2017), and MuMIn (Barton 2016).

RESULTS

By combining all available data from museum records, scientific literature, and state agency reports, we created a unique map showing eastern coyote expansion with 10-year time steps (Fig. 1). Among the states we studied, coyotes colonized New York and Ohio first (1930–1970s), whereas some counties in North Carolina were not colonized until the 2000s. The expansion by coyotes resulted in a wide range of colonization dates and duration of sympatry between deer and coyotes. For example, most of New York was completely colonized by 1980, while coyotes were just entering Florida at that time (Fig. 1).

Overall deer harvest increased since 1980 in most counties (Fig. 1), resulting in an index of population growth rate $\lambda \geq 1$ in all 7 periods (Fig. 3). For example, male harvest in North Carolina was estimated as 27,045 in 1981 and 82,144 in 2015; male harvest in Ohio was 19,363 in 1981 and 78,552 in 2015. We observed declines only in several counties (e.g., NJ

male harvest declined from 28,034 in 1995 to 15,243 in 2015; Fig. 1).

For all 7 periods, a highest-ranked model according to AIC weight (Tables 2 and 3) always was the simplest one and included only the intercept, spatial autocorrelation structure, and a random effect: $\ln(\lambda_{\text{male/total}})_{ij} = \beta_0 + u_j + \varepsilon_{ij}$. Hence, for all 14 models, no best model ever included the time since coyote arrival, any environmental covariates, or the interaction of time since coyote arrival and any environmental covariates.

DISCUSSION

We did not detect any negative association between colonizing eastern coyotes and white-tailed deer population growth rate across 6 eastern states over nearly a century. Instead, we documented a consistent rise in deer abundance simultaneous to coyote colonization across the region. Despite the relatively small-scale declines in some local deer populations attributed to coyote predation (Howze et al. 2009, VanGilder et al. 2009, Kilgo et al. 2014, Chitwood et al. 2015a, b), our study did not detect this relationship at a larger spatial and temporal scale.

The absence of an effect of coyotes on deer population growth was consistent over the course of coyote colonization.

Table 3. Relationship between eastern coyote colonization and white-tailed deer total harvest in 6 states in the eastern United States, 1981–2014. We present Akaike’s Information Criterion (AIC) values for the full models with and without spatial correlation and best models, model weights (w_i), and the number of parameters (K). The best model for every period was the one without covariates.

Period	Full model ^a , no spatial correlation				Full model with spatial correlation				The best model ^b		
	AIC	ΔAIC	w_i	K	AIC	ΔAIC	w_i	K	AIC	w_i	K
1981–1985	56.10	420.4	0.00	14	13.1	377.4	0.00	15	−364.3	1	4
1985–1990	−128.5	391.1	0.00	14	−142.8	376.8	0.00	15	−519.6	1	4
1990–1995	−237.1	386.8	0.00	14	−261.0	362.9	0.00	15	−623.9	1	4
1996–2000	−357.5	391.7	0.00	14	−361.1	388.1	0.00	15	−749.2	1	4
2000–2005	−369.3	462.5	0.00	14	−439.0	392.8	0.00	15	−831.8	1	4
2005–2010	−415.1	427.5	0.00	14	−456.0	386.6	0.00	15	−842.6	1	4
2011–2014	−160.1	421.8	0.00	14	−217.1	364.8	0.00	15	−581.9	1	4

^a The full model included state as a random effect and the covariates years since coyote arrival, average duration of snow pack, human population density, annual precipitation, precipitation seasonality, precipitation of driest quarter, mixed forest cover, low-intensity developed area, average tree canopy openness, and median and standard deviation of annual net primary productivity.

^b The highest-ranked model included the intercept, spatial autocorrelation structure, and a random effect of state.

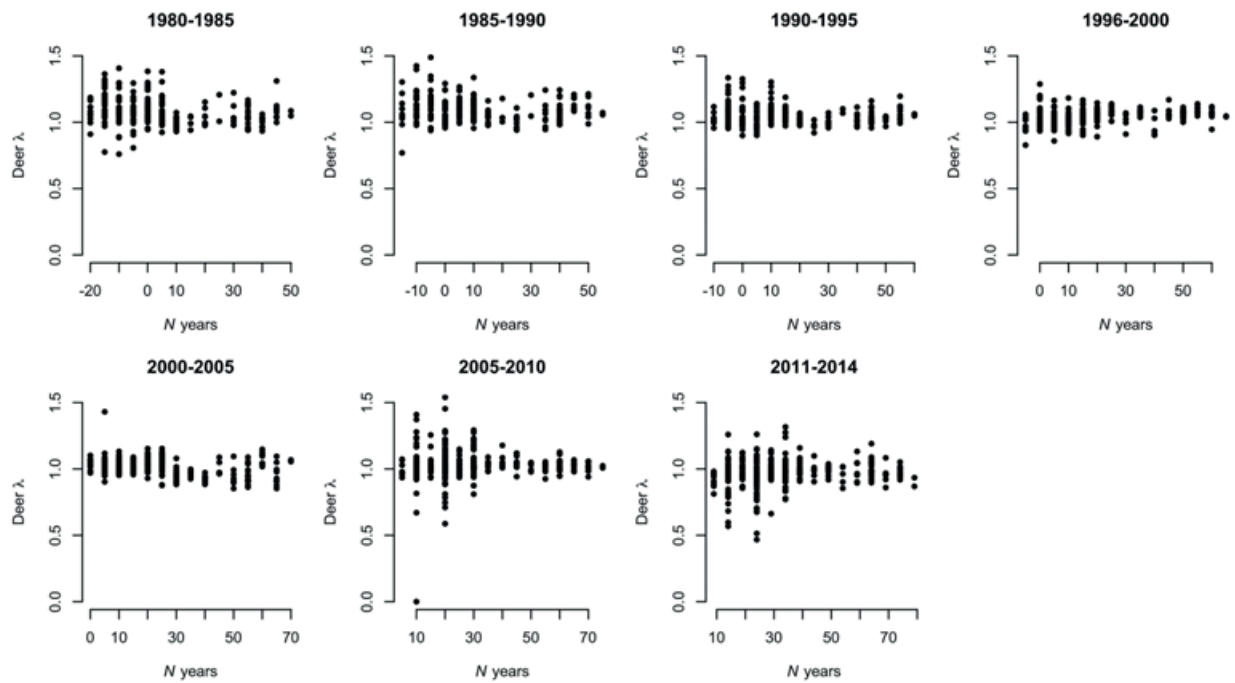


Figure 3. White-tailed deer population growth rate (λ ; based on male harvest data) as a function of number of years since coyote arrival (N years) for 7 periods to reflect various stages of coyote colonization in the eastern United States ($P > 0.05$ in all the time periods). Every dot is 1 county. Deer population growth $\lambda \sim 1$ indicates stationary population dynamics.

We did not document an effect of coyotes at the beginning of the study period, in 1981–1985, or later in 2011–2014 when coyotes were better established and more abundant across most of the study area (Fig. 3). Therefore, our prediction that deer population growth rate would be affected differentially over time since coyote arrival was not confirmed.

Among taxa and across ecological contexts, the degree of prey vulnerability to a novel predator varies widely. Our study did not measure coyote kill rates, but the lack of an effect of coyote presence on deer population growth across 6 states and nearly a century of time indicates the kill rate might not be great enough, or not directed towards life stages with high impact on population growth, to cause widespread, detectable declines in deer. Even when survival of fawns is low, deer populations may be sustained by high adult female survival (Robinson et al. 2014). Even though deer is prominent in eastern coyote diets (McVey et al. 2013, Chitwood et al. 2014, Swingen et al. 2015), and their predation on fawns is well documented (Kilgo et al. 2012, Chitwood et al. 2015b), the extent to which coyotes can hunt prey as large as an adult white-tailed deer (>50 kg) is debated (Chitwood et al. 2015a, Kilgo et al. 2016). Comparisons across the Carnivora order show an energetic threshold, with predators below 21.5 kg generally specializing in smaller prey (below predator mass) and predators above 21.5 kg energetically constrained to large prey (near or above predator mass, Carbone et al. 1999). Eastern coyote populations average 14–16 kg (Way 2007), well below the 21.5-kg threshold, suggesting they are too small to consistently kill adult deer. However, there are records of coyotes >21.5 kg (Way 2007), and this energetic threshold suggests there should be evolutionary selection for these larger animals. Indeed, a recent genomic study

discovered positive selection for wolf (*C. lupus*) genes associated with body size that had introgressed into eastern coyote populations (vonHoldt et al. 2016).

Our results indicate a lack of coyote effect on regional deer population growth and are in contrast with studies showing localized negative effects of coyotes on white-tailed deer populations (Howze et al. 2009, VanGilder et al. 2009, Kilgo et al. 2014). One mechanism that reconciles declines in local populations and stable or increasing overall abundance is spatial compensation (Schwartz et al. 2002, Harveson et al. 2004, Mills 2013). Rates of coyote predation and the effects of kill rate on deer dynamics are likely to vary across the landscape. For example, deer fawn protection from predation is directly linked to landscape heterogeneity (Gulsby et al. 2017). Under spatial compensation, increasing or stable populations in a heterogeneous landscape support declining populations through immigration, thereby dampening any coyote effects on overall regional deer growth rate (Harveson et al. 2004).

Although the temporal and spatial scale of our study required the use of proxies of relative changes in deer and coyote abundance, it is unlikely that we missed coyote effects on regional deer abundance. In particular, the consistent relationship of stationary or increasing numbers of deer harvested over time stood out despite nationwide declines in hunter numbers (Andersen et al. 2014) and despite varying social, market, and abiotic forces across time and space. Likewise, coyote numbers and distribution have increased over time in the eastern United States, a pattern detected in the rough distribution index (Fig. 2; Hody and Kays 2018). Collectively, our consistent results across a wide spatial scale (384 counties) support our inference that deer numbers

across the eastern United States have not been devastated by coyotes.

MANAGEMENT IMPLICATIONS

Our results underscore the value of considering broad spatial and temporal scales before initiating management actions that assume that an apex predator controls dynamics of an ungulate game species. Because we detected no signal for eastern coyotes causing a decline of white-tailed deer over time, our results imply that coyote removal would have little effect on increasing deer numbers in this region. Although coyote control may influence local deer dynamics for short periods of time in some situations, we do not expect coyote removal would be able to increase deer population size at large spatial scales.

ACKNOWLEDGMENTS

This study would not have been possible without data provided by multiple state agencies. We are grateful to C. McCoy, S. Prange, J. D. Kelly, J. E. Hurst, M. Schiavone, A. Burnett, D. Roberts, J. Shaw, R. Myers, D. Cobb, G. Albers, C. Olfenbittel, J. Butfiloski, C. Ruth, C. Morea, and A. Gulde from the state agencies. We thank C. Chitwood and M. Lashley for their constructive conversations. D. R. Diefenbach and J. Kilgo provided valuable suggestions for the analysis. We thank 2 reviewers, C. N. Jacques, and the Content Editor whose comments improved the manuscript. This study was funded by the United States Department of Defense, Fort Bragg Wildlife Branch, and the Fisheries, Wildlife, and Conservation Biology Program at North Carolina State University. LSM acknowledges National Science Foundation Division of Environmental Biology award 1743871.

LITERATURE CITED

- Andersen, O., H. K. Wam, A. Mysterud, and B. P. Kaltenborn. 2014. Applying typology analyses to management issues: deer harvest and declining hunter numbers. *Journal of Wildlife Management* 78:1282–1292.
- Barton, K. 2016. MuMIn: multi-model inference. R package version 1.15.6. <<https://cran.r-project.org/package=MuMIn>>. Accessed 20 Jan 2017.
- Batcheller, G. R., and P. Rixinger. 2011. Management plan for white-tailed deer in New York State 2012–2016. New York Department of Environmental Conservation, Albany, New York, USA.
- Brown, D. E., and M. R. Conover. 2011. Effects of large-scale removal of coyotes on pronghorns and mule deer productivity and abundance. *Journal of Wildlife Management* 75:876–882.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* 402:286–288.
- Cattadori, I. M., D. T. Haydon, S. J. Thirgood, and P. J. Hudson. 2003. Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. *Oikos* 100:439–446.
- Chitwood, M. C., M. A. Lashley, J. C. Kilgo, C. E. Moorman, and C. S. DePerno. 2015a. White-tailed deer population dynamics and adult female survival in the presence of a novel predator. *Journal of Wildlife Management* 79:211–219.
- Chitwood, M. C., M. A. Lashley, J. C. Kilgo, K. H. Pollock, C. E. Moorman, and C. S. DePerno. 2015b. Do biological and bedsite characteristics influence survival of neonatal white-tailed deer? *PLOS ONE* 10(3):e0119070.
- Chitwood, M. C., M. A. Lashley, C. E. Moorman, and C. S. DePerno. 2014. Confirmation of coyote predation on adult female white-tailed deer in the southeastern United States. *Southeastern Naturalist* 3:N30–N32.
- Crooks, J. A., and M. E. Soulé. 1999. Lag times in population explosions of invasive species: causes and implications. Pages 103–125 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. *Invasive species and biodiversity management*. Kluwer Academic Press, Dordrecht, The Netherlands.
- Dietz, A. J., C. Kuenzer, and S. Dech. 2015. Global SnowPack: a new set of snow cover parameters for studying status and dynamics of the planetary snow cover extent. *Remote Sensing Letters* 6:844–853.
- Dillman, D. A. 2011. Mail and internet surveys: the tailored design method — 2007 update with new internet, visual, and mixed-mode guide. Second edition. John Wiley and Sons, Hoboken, New Jersey, USA.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46.
- Fener, H. M., J. R. Ginsberg, E. W. Sanderson, and M. E. Gompper. 2005. Chronology of range expansion of the coyote, *Canis latrans*, in New York. *Canadian Field-Naturalist* 119:1–5.
- Fisk, D. L., L. C. Latta, R. A. Knapp, and M. E. Pfrender. 2007. Rapid evolution in response to introduced predators I: rates and patterns of morphological and life-history trait divergence. *BioMed Central Evolutionary Biology* 7:7–22.
- Gulsby, W. D., J. C. Kilgo, M. Vukovich, and J. A. Martin. 2017. Landscape heterogeneity reduces coyote predation on white-tailed deer fawns. *Journal of Wildlife Management* 81:601–609.
- Gulsby, W. D., C. H. Killmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. *Wildlife Society Bulletin* 39:248–255.
- Harveson, P. M., R. R. Lopez, N. J. Silvy, and P. A. Frank. 2004. Source-sink dynamics of Florida key deer on Big Pine Key, Florida. *Journal of Wildlife Management* 68:909–915.
- Hayes, R. A., H. F. Nahrung, and J. C. Wilson. 2006. The response of native Australian rodents to predator odours varies seasonally: a by-product of life history variation? *Animal Behaviour* 71:1307–1314.
- Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86:2135–2144.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Hody, J. W., and R. Kays. 2018. Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. *ZooKeys* 759:81–97.
- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Howze, M., L. Conner, R. Warren, and K. Miller. 2009. Predator removal and white-tailed deer recruitment in southwestern Georgia. *Proceedings of the Annual Conference / Southeastern Association of Fish and Wildlife Agencies* 63:17–20.
- Hudgens, B. R., and D. K. Garcelon. 2011. Induced changes in island fox (*Urocyon littoralis*) activity do not mitigate the extinction threat posed by a novel predator. *Oecologia* 165:699–705.
- Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in Southeastern Idaho. *Wildlife Monographs* 178:1–33.
- Imperio, S., M. Ferrante, A. Grignetti, G. Santini, and S. Focardi. 2010. Investigating population dynamics in ungulates: do hunting statistics make up a good index of population abundance? *Wildlife Biology* 16:205–214.
- Kays, R. W., M. E. Gompper, and J. C. Ray. 2008. Landscape ecology of eastern coyote based on large-scale estimates of abundance. *Ecological Applications* 18:1014–1027.
- Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. *Journal of Wildlife Management* 76:1420–1430.
- Kilgo, J. C., M. Vukovich, M. J. Conroy, H. S. Ray, and C. Ruth. 2016. Factors affecting survival of adult female white-tailed deer after coyote establishment in South Carolina. *Wildlife Society Bulletin* 40:747–753.

- Kilgo, J. C., M. Vukovich, H. S. Ray, C. E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. *Journal of Wildlife Management* 78:1261–1271.
- Lambin, X., C. J. Krebs, R. Moss, N. C. Stenseth, and N. G. Yoccoz. 1999. Population cycles and parasitism. *Science* 286:2425.
- Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. *Proceedings of the National Academy of Sciences* 109:10942–10947.
- Levi, T., and C. Wilmers. 2012. Wolves—coyotes—foxes: a cascade among carnivores. *Ecology* 93:921–929.
- Levy, S. 2012. Rise of the coyote: the new top dog. *Nature* 485:296–297.
- Main, M. B., S. F. Coates, and G. M. Allen. 2000. Coyote distribution in Florida extends southward. *Florida Field Naturalist* 28:201–203.
- McVey, J. M., D. T. Cobb, R. A. Powell, M. K. Stoskopf, J. Boling, L. P. Waits, and C. E. Moorman. 2013. Diets of sympatric red wolves and coyotes in northeastern North Carolina. *Journal of Mammalogy* 94:1141–1148.
- Messier, F., C. Barrette, and J. Huot. 1986. Coyote predation on a white-tailed deer population in southern Quebec. *Canadian Journal of Zoology* 64:1134–1136.
- Mills, L. S. 2013. Conservation of wildlife populations. Demography, genetics, and management. Wiley-Blackwell, West Sussex, United Kingdom.
- Myers, R. T. 2013. 2012–13 hunter harvest survey report. North Carolina Wildlife Resources Commission, Raleigh, USA.
- Nelson, M. E., and L. D. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. *Journal of Wildlife Management* 50:471–474.
- Newby, J. R., L. S. Mills, T. K. Ruth, D. H. Pletscher, M. S. Mitchell, H. B. Quigley, K. M. Murphy, and R. DeSimone. 2013. Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. *Biological Conservation* 159:230–239.
- Newsome, T. M., and W. J. Ripple. 2015. A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology* 84:49–59.
- Novaro, A. J., M. C. Funes, and R. S. Walker. 2005. An empirical test of source-sink dynamics induced by hunting. *Journal of Applied Ecology* 42:910–920.
- Ozoga, J. J., and L. W. Gysel. 1972. Response of white-tailed deer to winter weather. *Journal of Wildlife Management* 36:892–896.
- Patterson, B. R., and F. Messier. 2003. Age and condition of deer killed by coyotes in Nova Scotia. *Canadian Journal of Zoology* 81:1894–1898.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2017. nlme: linear and nonlinear mixed effects models. R package version 3.1–131. <<https://CRAN.R-project.org/package=nlme>>. Accessed 22 Jan 2017.
- Robinson, K. F., D. R. Diefenbach, A. K. Fuller, J. E. Hurst, and C. S. Rosenberry. 2014. Can managers compensate for coyote predation of white-tailed deer? *Journal of Wildlife Management* 78:571–579.
- Ruth, C., and J. Cantrell. 2016. South Carolina deer harvest report. South Carolina Department of Natural Resources, Columbia, USA.
- Schreiber, S. J., and M. Vejdani. 2006. Handling time promotes the coevolution of aggregation in predator-prey systems. *Proceedings of the Royal Society B: Biological Sciences* 273:185–191.
- Schwartz, M. K., L. S. Mills, K. S. McKelvey, L. F. Ruggiero, and F. W. Allendorf. 2002. DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. *Nature* 415:520–522.
- Swingen, M. B., C. S. DePerno, and C. E. Moorman. 2015. Seasonal coyote diet composition at a low-productivity site. *Southeastern Naturalist* 14:397–404.
- VanGilder, C. L., G. R. Woods, and K. V. Miller. 2009. Effects of an intensive predator removal on white-tailed deer recruitment in northeastern Alabama. *Proceedings of the Annual Conference / Southeastern Association of Fish and Wildlife Agencies* 63:11–16.
- vonHoldt, B. M., R. Kays, J. P. Pollinger, and R. K. Wayne. 2004. Admixture mapping identifies introgressed genomic regions in North American canids. *Molecular Ecology* 25:2443–2453.
- Vreeland, J. K., D. R. Diefenbach, and B. D. Wallingford. 2004. Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns. *Wildlife Society Bulletin* 32:542–553.
- Wallach, A. D., W. J. Ripple, and S. P. Carroll. 2015. Novel trophic cascades: apex predators enable coexistence. *Trends in Ecology and Evolution* 30:146–153.
- Way, G. 2007. A comparison of body mass of *Canis latrans* (coyotes) between eastern and western North America. *Northeastern Naturalist* 14:111–124.
- Weeks, J. L., G. M. Tori, and M. C. Shieldcastle. 1990. Coyotes (*Canis latrans*) in Ohio. *Ohio Journal of Science* 1990:1–4.
- Weinstein, M. S. 1977. Hares, lynx, and trappers. *American Naturalist* 111:806–808.
- Whitaker, J. O., and W. J. Hamilton. 1998. Mammals of the eastern United States. Cornell University Press, Ithaca, New York, USA.
- Winterhalder, B. P. 1980. Canadian fur bearer cycles and Cree-Ojibwa hunting and trapping practices. *American Naturalist* 115:870–879.
- Zuur, A. F., E. N. Leno, N. J. Walker, A. A. Saveliev, G. M. Smith, E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York, New York, USA.

Associate Editor: Christopher Jacques.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.