



Research Article

Effects on White-Tailed Deer Following Eastern Coyote Colonization

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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

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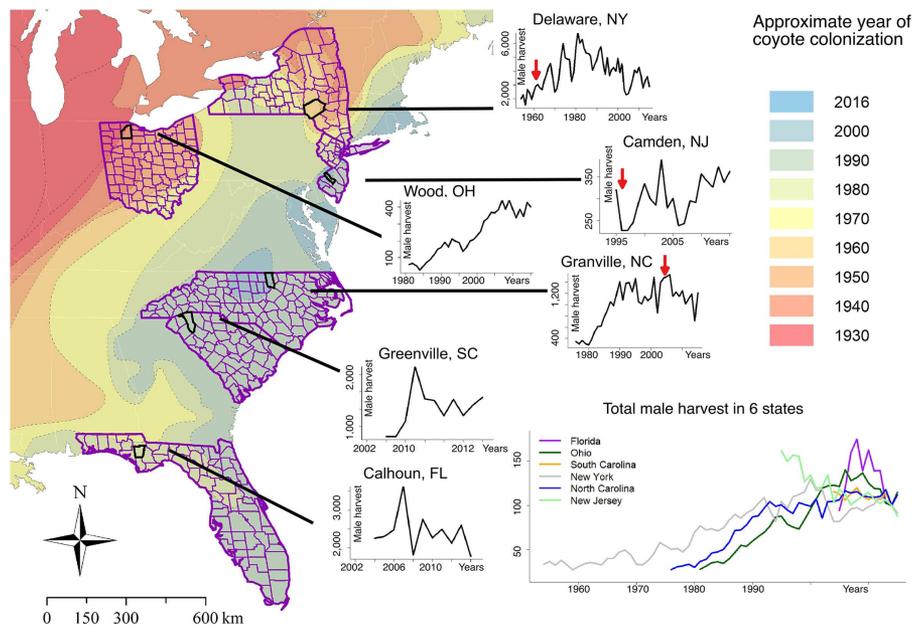


Figure 1. Coyote colonization and white-tailed deer harvest in 1930–2016 (Hody and Kays 2018). In each of 6 states, we plotted male deer harvest in a randomly chosen county as an example. Red arrows in Delaware, New York; Camden, New Jersey; and Granville, North Carolina, show the time of coyote arrival. 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-

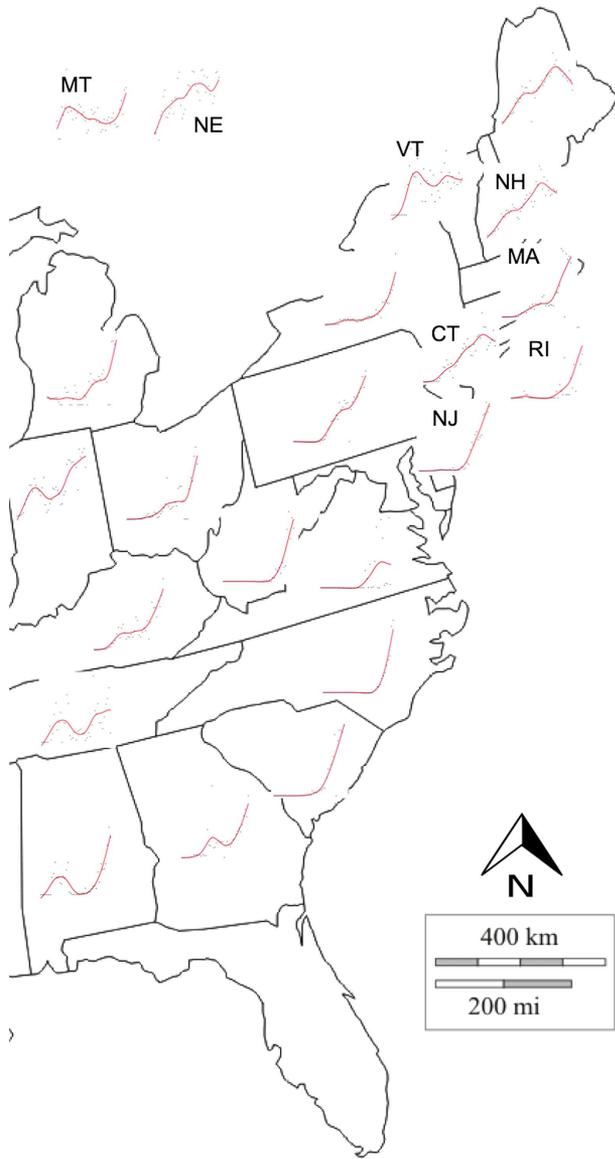


Figure 2. Coyotes harvested by trappers in 20 eastern United States from 1970 to 2015 showing a consistent increase across the region. We include 2 examples of western states for comparison. The red lines highlight smoothed relationship through annual harvest numbers (black dots). Scale of y-axis varies 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.

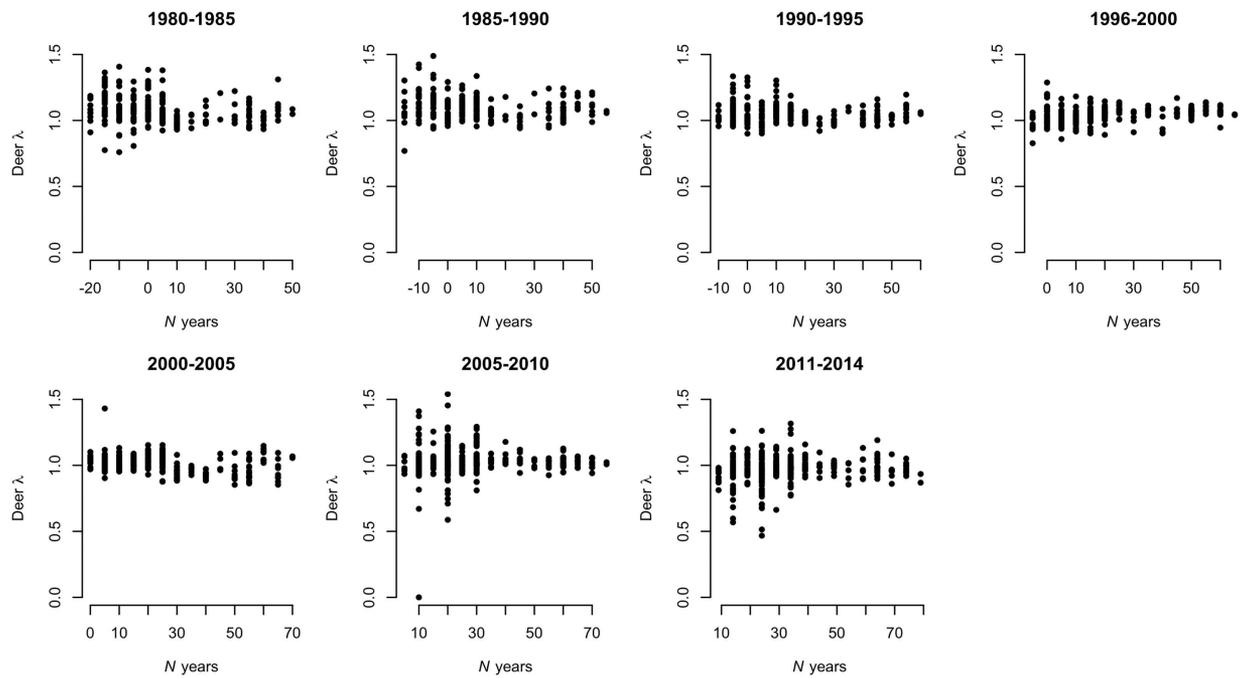


Figure 3. White-tailed deer population growth rate (λ ; based on male harvest data) as a function of number of years since coyote arrival (N years) for 7 periods to reflect various stages of coyote colonization in the eastern United States ($P > 0.05$ in all the time periods). Every dot is 1 county.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

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SUPPORTING INFORMATION

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



Letter to the Editor

Coyotes and White-Tailed Deer Populations in the East: A Comment on Bragina et al. (2019)

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Nearly 10 years ago, Kilgo et al. (2010) published a commentary that raised the question, “Can coyotes affect deer populations in southeastern North America?” Since then, numerous field studies have shed light on, if not unequivocally answered, that question. Those studies, which have spanned the region in question, have been virtually unanimous in concluding that coyotes (*Canis latrans*) can indeed influence deer population dynamics through heavy predation pressure on neonate deer. These were all field studies, conducted at a particular location and at a particular time. In contrast, Bragina et al. (2019) assembled an 87-year dataset from eastern states as widespread as New York and Florida, USA, to assess the question of whether coyotes can affect white-tailed deer (*Odocoileus virginianus*) populations at large spatial scales in the East. From those data, they concluded that “coyotes are not controlling deer populations at a large spatial scale in eastern North America” (Bragina et al. 2019:916). We commend Bragina et al. (2019) for examining the question at a large scale. However, a combination of problems inherent in their approach and in their data led to erroneous conclusions and overly simplistic inferences. We are concerned that assertions by Bragina et al. (2019) may perpetuate misconceptions among deer managers and the public about the nature of the deer-coyote dynamic in the region and may therefore be potentially harmful to the resource. Here we detail our primary concerns with Bragina et al. (2019).

Use of Deer Harvest Data to Index Deer Population Size

Bragina et al. (2019) used deer harvest data as a proxy for relative abundance, an approach they acknowledged had limitations in tracking true abundance, but they justify the approach by citing Cattadori et al. (2003) and Imperio et al. (2010). Although Cattadori et al. (2003) validated the use of harvest data as an indirect measure of abundance, the authors indicated the applicability of their results were

limited to red grouse (*Lagopus lagopus scotica*) in the United Kingdom, a species and study system much different from white-tailed deer in the eastern United States. In contrast, Imperio et al. (2010) focused on 5 ungulate species in Italy, making their findings more relevant to Bragina et al. (2019). Imperio et al. (2010), however, suggested that the use of bag records not corrected for hunting effort and without any previous validation, conditions not met by Bragina et al. (2019), could produce misleading estimates of abundance. Rosenberry and Woolf (1991) similarly reported that white-tailed deer harvest data adjusted for hunter effort had a more linear relationship with population size than did the overall harvest.

Without adjustments for hunter effort throughout the study period, several sources of potential bias could decrease the reliability of deer harvest data as an index of deer abundance. One source of bias, which Bragina et al. (2019) acknowledged, is the changes in deer management regulations by state wildlife agencies during the study period. Bragina et al. (2019:table 1) provided a summary of the most important deer management regulation changes for the 6 states used in their analysis. In 5 of those states, Bragina et al. (2019) reported regulation changes that expanded hunter opportunity (FL was the only state that did not increase opportunity during the study), which positively affects hunter harvest (Van Deelen et al. 2010). Conversely, 3 states also decreased opportunity for male harvest during the study period, 2 via antler size restrictions (NY, FL) and 1 via bag limit or season restrictions (NJ). We contend that the objective of all of these regulation changes was to alter harvest rates which, if successful, confounded the relationship between harvest data and population size.

The use of data from South Carolina is particularly concerning, especially given its timeframe, and offers a useful case study on how deer harvest can be confounded by regulation changes. Specifically, Bragina et al. (2019:table 1) reported that in 2004, the first year in their dataset, South Carolina began reducing the number of days on which deer of either sex could be harvested. These reductions continued periodically through 2014 and were implemented in response to a decline in the deer population, which the reductions

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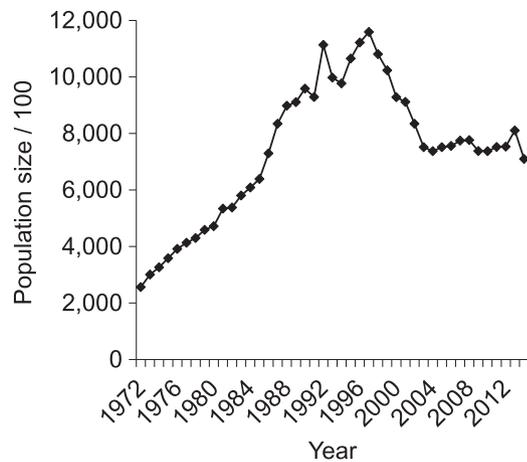


Figure 1. Estimated statewide deer population size in South Carolina, USA, 1972–2014 (Ruth and Cantrell 2018).

apparently slowed or halted (Fig. 1). Clearly, from 2004–2014, South Carolina’s deer harvest, which steadily declined because of reduced hunter opportunity (Ruth and Cantrell 2018), did not reflect the deer population trend, which had stabilized because of reduced harvest. Furthermore, South Carolina’s deer harvest estimates were derived from an annual hunter survey, which the state’s Deer Project Coordinator indicated is robust at the state level but sufficiently imprecise at the county level (as Bragina et al. [2019] used it) as to render its use highly questionable at that level (C. R. Ruth, South Carolina Department of Natural Resources, personal communication). Thus, our main contentions with their approach of using harvest data as an index of deer abundance are that use of unadjusted deer harvest numbers as a proxy for abundance is not supported by the literature and there are a number of factors (mainly changes in harvest regulations during the study period) that would bias deer harvest over time, even if this metric were a suitable proxy for abundance.

Use of Time Since Coyote Arrival to Index Coyote Abundance

Another limitation of this study is the use of time since coyote arrival to evaluate the effect of coyotes on deer populations. Although we applaud the attempt of Bragina et al. (2019) to depict coyote colonization through space and time, we think the use of time since arrival as a predictor variable for understanding potential effects of coyotes on deer populations relies on faulty assumptions. For example, the assumption that coyotes would affect deer linearly through time does not seem reasonable given coyote population growth, and by extension their potential to affect prey, likely varies spatially. Studies have demonstrated abundance of eastern coyotes varies with landscape composition and configuration (Kays et al. 2008, Cherry et al. 2017). Therefore, variation in local and regional landscape conditions likely would result in a mosaic of population growth rates and time to population stabilization. Bragina et al. (2019) acknowledged that their study area spanned a range of climatic, elevational, and land cover ranges among states but

apparently assumed coyote population growth among the 6 states was similar and linear. Additionally, coyote abundance can be regulated by food availability and social factors associated with territoriality (Gese et al. 1989, Knowlton et al. 1999). Thus, coyotes do not have infinite growth potential. The test of a linear effect of time since coyote arrival on deer populations assumes that any negative influence of coyotes on deer populations continues linearly through time. These assumptions seem unrealistic, and it seems more likely that if coyotes negatively influenced deer populations, the effects eventually stabilized as coyotes became saturated across the landscape and their populations reached carrying capacity. Furthermore, as demonstrated by Bragina et al. (2019:figure 2), if one assumes harvest reflects abundance, as the authors did with regard to deer harvest, coyote population growth is nonlinear and, in fact, appears to be exponential in numerous states. These issues are likely compounded by the mismatch in scale of the timing of coyote colonization and deer harvest records, as the authors reported changes in deer abundance from 1981–2014 in states colonized by coyotes during the 1910s–1970s.

Incongruity Between Time Periods of Analysis and Timing of Coyote Influence

The deer harvest data Bragina et al. (2019) used from Florida, Ohio, and South Carolina spanned time periods after the establishment of coyotes, allowing for the possibility that effects of coyotes on deer populations had already occurred. For example, the time period Bragina et al. (2019) used for South Carolina was 2004–2016. As described by Kilgo et al. (2010), South Carolina’s deer population peaked in the mid-1990s after a period of increase following the restocking programs of the 1950s and 1960s. From 1997 through 2004, coincident with the establishment and increase of coyotes in the state, but just prior to the period examined by Bragina et al. (2019), the deer population declined by about 35%. Extending Kilgo et al. (2010:figure 1) to 2014 (the limit of the Bragina et al. [2019] data; Fig. 1) demonstrates that the statewide deer population in fact remained relatively stable during the period Bragina et al. (2019) used; the potential effect of coyotes on the population (i.e., the negative relationship that their models failed to detect) had already occurred, prior to the timeframe covered by their data. Similarly, by their own estimation, the data used by Bragina et al. (2019) for Florida (2005–2016) covers a period 15–25 years after coyote arrival and their data for Ohio covers a period 11–51 years after coyote arrival. Therefore, as with South Carolina, their data may simply have been for the wrong time period. Failure to detect a relationship between coyotes and deer does not necessarily mean that one does not exist, only that it was not evident in the data they used.

Regional Differences in Predation Rate

Any effect of coyotes on deer likely varies spatially, independent of time since coyote arrival, because habitat

selection of eastern coyotes is nonrandom (Hinton et al. 2015, Stevenson et al. 2018), and diets can vary substantially, even at small spatial scales (Etheredge et al. 2015, Ward et al. 2018). Additionally, landscape composition and configuration can influence coyote abundance (Cherry et al. 2017) and their effects on fawn survival (Gulsby et al. 2017, Gingery et al. 2018). This variation and resultant regional trends complicate analysis of coyote effects on deer at the scale of eastern North America. For example, predation pressure appears generally greater in the South than in the Midwest and Northeast (Fig. 2). Among studies assessing cause-specific mortality on neonatal deer, the coyote-specific predation rate (percentage of all neonates in the sample that were depredated by coyotes) averaged 16% among 9 studies in the Midwest and Northeast and 44% among 10 studies in the South (Fig. 2). Speculation on mechanisms influencing this regional pattern are beyond the scope of this commentary. But the very existence of this pattern, combined with regional differences in timing of coyote arrival (i.e., earlier in the North than the South), requires careful interpretation of results when data are pooled across regions. For example, Bragina et al. (2019) report population change (λ) ≥ 1 for all 7 time periods analyzed. Visual inspection of their figure 3 (λ values were not provided) suggests that mean values for λ were quite high for periods during the 1980s and 1990s, when deer populations range-wide were growing

rapidly, but these values tended to be lower for later periods, especially the last period (2011–2014; Bragina et al. 2019:figure 3). For early periods in figure 3, counties that had been occupied <30 years were in northern states where predation tends to be low, whereas in later periods, those counties were in southern states where predation tends to be greater. As expected then, λ values during early periods in counties <30 years since arrival were >1.0 , but for later periods, in counties <30 years since arrival, λ tended to be <1.0 . Bragina et al. (2019) seem to have disregarded as unimportant what appear to be roughly half or more of the 384 counties in their dataset with λ values <1.0 since 2005.

Interpretation of Negative Results

Given that their conclusion is based on the lack of detecting an effect, we are concerned that Bragina et al. (2019) did not qualify the strength of the conclusion, other than acknowledging that coyotes may affect deer populations in isolated local situations. We think it is prudent to exercise caution when interpreting negative results, given that the failure to detect a signal could result from flaws or limitations in experimental design or procedures. Negative results can stem from lack of statistical power, inadequate or mismatched spatial or temporal scales of the investigation relative to the scale of the process under study, failure to



Figure 2. Coyote-specific predation rates (% of neonates in sample that were depredated by coyotes) among studies conducted in the core range of white-tailed deer on areas where coyotes and bobcats (*Lynx rufus*) were the primary predators (i.e., black bears [*Ursus americanus*], wolves [*Canis lupus*], and cougars [*Puma concolor*] were not present; Cook et al. 1971, Carroll and Brown 1977, Garner et al. 1976, Bartush and Lewis 1981, Huegel et al. 1985, Nelson and Woolf 1987, Long et al. 1998, Brinkman et al. 2004, Burroughs et al. 2006, Rohm et al. 2007, Saalfeld and Ditchkoff 2007, Hiller et al. 2008, Piccolo et al. 2010, Grovenburg et al. 2011, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015b, Nelson et al. 2015, Watine and Giuliano 2016).

select the correct variables or to characterize them adequately, or inappropriate model assumptions (e.g., linear model when process of interest is non-linear). Obviously, establishing a study at the scale at which one thinks the process occurs and reporting negative results is valid. Nonetheless, we suggest the limitations of the approach should be considered thoroughly before drawing strong inference from the lack of detection of a signal. The fact that none of the models fit in this study had significant predictive power (as evidenced by the fact that the null model was universally the most supported model) should further induce caution. Considering the issues described here associated with the deer population response variable and the time since coyote arrival predictor variable, it is not surprising they were not related.

Potential Harm to the Resource

Perhaps our greatest concern lies with the implications of asserting that “coyotes are not controlling deer populations at a large spatial scale in eastern North America” (Bragina et al. 2019:916). We do not dispute that statement *per se* because it has been recognized that hunter harvest, not predation, is the single most important factor controlling (or capable of controlling) white-tailed deer populations. However, such statements represent a considerable oversimplification of a complex predator-prey dynamic and minimize the important role that coyotes have come to play in the population dynamics of white-tailed deer in eastern North America during recent decades. Every published study of cause-specific fawn mortality conducted in southeastern North America since coyotes have been present, not including those where coyotes were controlled, has demonstrated very high predation rates by coyotes, leading to recruitment rates much lower than before coyotes arrived (Saalfeld and Ditchkoff 2007, Kilgo et al. 2012, Jackson and Ditchkoff 2013, Chitwood et al. 2015b, Nelson et al. 2015, Watine and Giuliano 2016). Yet Bragina et al. (2019:922) dismiss (or fail to cite) this body of literature as representing only “localized negative effects,” which they propose are somehow overcome through spatial compensation, an explanation we consider implausible given the size of the study areas considered and the dispersal capabilities of white-tailed deer. With recruitment as low as these studies have shown, heavy harvest of adult female deer (which prior to the arrival of coyotes was often inadequate to control the population) is in many situations no longer sustainable. Reduced harvest of adult female deer is necessary to mitigate effects of increased fawn predation by coyotes (Robinson et al. 2014), and reductions in adult female harvest may be inadequate to offset population declines in some situations (Chitwood et al. 2015a). If harvest is not reduced in such areas, populations decline, and indeed several states have implemented state-wide regulations restricting antlerless harvest in response to declining recruitment rates (e.g., AL, GA, SC). Population reduction may be beneficial where deer are overabundant but not necessarily where they occur at low density. Thus, although it is true that coyotes, strictly speaking, “are not controlling

deer populations” (Bragina 2019:916), the important point for wildlife managers to consider is that coyotes nevertheless have influenced significant changes in harvest planning and hunter opportunity. Because Bragina et al. (2019) did not qualify or expound on their conclusions about the effects of coyotes on deer, readers are left to assume that because the authors did not detect a relationship between them, coyotes need not be considered in deer management at all.

Conclusion

The number of uncertainties associated with the data and the scope of the problems with the analysis employed by Bragina et al. (2019:916) were of such magnitude as to render unwarranted their sweeping conclusion “that coyotes are not controlling deer populations at a large spatial scale in eastern North America.” Furthermore, we contend that, although the scale of their question might be interesting from a basic science standpoint, it should not be used to inform deer management policy, which should be implemented at a statewide, or smaller, scale. More concerning, however, was the manner in which Bragina et al. (2019) oversimplify the complexity of this important wildlife management issue, boiling it down to a binary question of whether or not coyotes directly control deer, when in fact the issue is far more nuanced than that, with hunter harvest continuing to play a central role. As recent researchers have demonstrated, after the arrival of coyotes, many Southeastern deer populations have not been able to sustain harvest at levels previously insufficient to control those populations (Kilgo et al. 2012, Robinson et al. 2014, Chitwood et al. 2015a). Declines in these populations are thus not attributable solely to coyotes but to the combination of coyote predation and high harvest rates. In contrast, northern populations seem less affected, presumably because of lower predation and antlerless harvest rates. Still, coyote predation represents an important influence on deer populations that should not be dismissed but instead be clearly understood and accounted for in harvest management because it plays a key role in the dynamics of these populations.

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Letter to the Editor

White-Tailed Deer and Coyote Colonization: A Response to Kilgo et al. (2019)

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We appreciate the comments by Kilgo et al. (2019) on our recent paper and welcome the opportunity to expand the discussion of the effects of coyotes (*Canis latrans*) on white-tailed deer (*Odocoileus virginianus*) in eastern North America. This exchange allows us to reaffirm and elaborate on our finding that coyotes have not had large-scale effects on white-tailed deer population growth in eastern North America.

A scientific evaluation of how any predator affects prey numbers is typically a complex challenge that requires a variety of approaches at a variety of scales. The evaluation becomes especially challenging for populations that interact across a complex and variable landscape because the dynamics of individual populations affect each other through immigration and emigration. Thus, for vagile wildlife species with a broad distribution, studies of single populations cannot fully answer how the predator affects the prey species across the larger connected landscape. Of course, intensive and detailed site- and time-specific studies on local predator-prey dynamics are critically important, and necessary to a mechanistic understanding of processes of predation. By themselves, however, a collection of such local studies over short time periods cannot determine how predator-prey dynamics play out over large spatial and temporal scales.

Coyotes and white-tailed deer in the eastern United States are an example of a spatially complex predator-prey system. Following the extinction of wolves (*Canis lupus*) and cougars (*Puma concolor*) in the region, coyotes colonized all eastern states over the last half-century (Hody and Kays 2018). Coyotes now occupy all land cover types in the region, where they overlap, and prey on, white-tailed deer. In Bragina et al. (2019), we noted site-specific field studies conducted (Vreeland et al. 2004, Kilgo et al. 2012,

Chitwood et al. 2015) on coyotes and deer in various parts of this system and agree that several of these studies show local effects of coyotes on white-tailed deer vital rates or numbers (Vreeland et al. 2004, Howze et al. 2009, Chitwood et al. 2015); however, the results of these studies have not always been consistent, demonstrating the predator-prey dynamic is variable over space or time. For example, Kilgo et al. (2016:747) concluded that “predation by coyotes on adult females was not important,” Kilgo et al. (2014:1261) stated that “despite an initial increase, the overall effect of coyote removal on neonate [deer] survival was modest,” and Gulsby et al. (2017) reported that coyote predation on fawns depended on habitat fragmentation. In short, the full collection of field studies reveal coyote-deer interactions in certain places at certain times, but they were not designed to answer the question addressed in Bragina et al. (2019): How have coyotes affected deer population growth from 1981 to 2014 across multiple states in the eastern United States?

In answering this question, nothing in Bragina et al. (2019) dismissed the valuable time- and place-specific field studies of coyotes and white-tailed deer to which Kilgo et al. (2019) referred. It is apparent the concerns of Kilgo et al. (2019) arise from an incomplete appreciation of the different strengths, scope of inference, and types of questions that can be addressed with local and time-specific field studies, versus broader space and time studies such as ours.

Faced with the overarching question of whether coyotes have affected white-tailed deer population dynamics over 531,312 km² and more than 3 decades, we would ideally use rigorously collected population estimates of both species from across the entire region. These estimates exist in vanishingly few cases. Therefore, with full awareness and appreciation of the promise and pitfalls of indices relative to rigorous estimates of abundance (Pollock et al. 2002, Mills et al. 2005, Johnson 2008), we used the only data available over time and space from 6 state agencies: indices of trends in white-tailed

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deer and coyote relative abundance. These indices are most reliable when seeking strong signals across large data sets (e.g., broad-scale disease outbreaks) and are appropriate for detecting the large (1–2 orders of magnitude) changes in prey populations seen in other natural experiments where new predators are added or reintroduced to a system (Levi et al. 2012, Ripple et al. 2014). In this analysis, we documented no negative association between relative numbers of coyotes and white-tailed deer across 6 states over more than 3 decades, supporting our conclusion that coyotes have not had large effects on white-tailed deer numbers across time and space in the eastern United States.

In addition to reaffirming our conclusions, we address specific concerns of Kilgo et al. (2019). Kilgo et al. (2019) suggested that harvest records should be adjusted for amount of harvest effort, which, in turn, could depend on changes in hunting regulations. We initially attempted to account for harvest effort using 3 states for which we could obtain metrics of effort, and detected no change in results. We decided there was little value in a correction because of incomplete records at the wildlife management agencies, and the multiple components and nuances of defining effort (e.g., regulations on baiting, weapon type, land access, hunter efficiency). Nevertheless, we noted that deer harvest regulation changes expanded hunter opportunity in 5 of 6 states over the time period we examined. Because agencies typically increase hunter effort in response to an increase (not decrease) in the hunted species, expanded hunting opportunities adds further qualitative support that agencies were not adjusting white-tailed deer harvest as might be expected if coyotes were causing a collapse of the deer population.

Kilgo et al. (2019:1637) expressed concerns that our analytic framework did not account for spatial variability in coyote population growth, and that we assumed “that coyotes would affect deer linearly through time.” We never made this assumption. In Bragina et al. (2019:920), we used log-transformed deer population growth rate (λ): $\ln(\lambda_{\text{deer}}) = \beta_0 + \beta_1 \text{coyote}_{ij} + \beta_2 \text{snow cover}_{ij} + \beta_3 \text{human population}_{ij} + \text{other covariates}$. This formula makes no assumptions that coyotes in any particular area have the same inherent growth rate or density-dependent function (e.g., from territoriality or food). Our approach asks, across the full spectrum of sites and time, whether time since coyote arrival predicts deer population trends.

Kilgo et al. (2019:1637) claimed that “Bragina et al. (2019) acknowledged that their study area spanned a range of climatic, elevational, and land cover ranges among states but apparently assumed coyote population growth among the 6 states was similar.” Their assertion is incorrect; our statistical models incorporated county-specific climate and land cover covariates to account for variance of coyote population expansion in the context of spatial differences in snow cover, human population density, precipitation, land cover, canopy openness and net primary productivity.

Kilgo et al. (2019) expressed concern that eastern coyotes may have negatively affected white-tailed deer harvest outside of the times we analyzed. Their hypothesis cannot be supported or rejected for a given data set. Moreover, our

paper did not discuss coyote effect on deer before the time period which our study spanned (i.e., before 2004 in SC).

Kilgo et al. (2019) stated that we did not acknowledge regional variability in coyote predation rate. This point is incorrect because the linear mixed model framework used in our analysis accounted for regional variability using a random effect for state. Of course, some of the 384 counties had deer $\lambda < 1$, but the average deer λ across 384 counties in 6 states was >1 in the presence of coyotes (e.g., Bragina et al. 2019:figure 1).

In various parts of their critique, Kilgo et al. (2019) assembled lists of individual field studies in the southeastern United States that documented high predation rates by coyotes, but these do not counter the implication of our results. First principles of population ecology distinguish between changes in individual vital rates and changes in population numbers. Predation rates can be massive without affecting population growth, depending on a host of factors, including compensation of mortality (via survival, reproduction, or immigration), reproductive values of individuals killed, and relative importance of specific vital rates to population growth (Morris and Doak 2002, Mills 2013). Local mortalities due to predation do not equal range-wide predator control of prey numbers.

Kilgo et al. (2019) ended their critique with a focus on implications of our paper for conservation and wildlife management. Their arguments are perplexing and seemingly self-contradictory. For example, in a single sentence Kilgo et al. (2019:1639) agrees verbatim with our main conclusion but then closes with a separate point as if it counters the first: “Thus, although it is true that coyotes, strictly speaking, ‘are not controlling deer populations’ the important point for wildlife managers to consider is that coyotes nevertheless have influenced significant changes in harvest planning and hunter opportunity.” The implication is that coyote importance to wildlife management at local scales somehow diminishes our result that deer are not being controlled at the large spatial scale. Rather, we believe that these ideas are not in opposition to each other: no evidence connects coyote colonization to range-wide white-tailed deer collapse in the eastern United States, and coyotes have had and do have local effects on deer and other prey and so absolutely should continue to be considered when planning harvest and other conservation management activities.

Thus, we believe that Kilgo et al. (2019) have created a redundant and unnecessary dichotomy between our results (that over the full scope of space and time since coyotes colonized the eastern United States, no white-tailed deer collapse has occurred) and their concern (that coyotes can locally affect white-tailed deer in the eastern United States). We believe these are entirely compatible views. Although we detected no signal of range-wide deer collapse influenced by coyotes, we remain fully aware that predators, such as coyotes, are capable of affecting numbers of their prey in fundamental ways that can, for example, affect trophic cascades (Crooks and Soule 1999, Levi and Wilmers 2012) or influence local population declines (Witczuk et al. 2013, Chitwood et al. 2015).

We hope this exchange has been constructive and can lead to future discussion around the relationships between coyotes and white-tailed deer in the eastern United States. We suggest future research emphasize the factors influencing local- and regional-scale variation in coyote-deer dynamics, whether related to land cover, coyote densities, deer densities, coyote harvest, or some combination. Moreover, we recommend wildlife managers monitor white-tailed deer and coyote populations locally and appropriately adjust harvest regulations in the presence of predation by coyotes and other species.

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