

ARTICLE**Macrosystems Ecology**

Urbanization and primary productivity mediate the predator–prey relationship between deer and coyotes

Arielle W. Parsons¹  | Krishna Pacifici¹ | Jonathan C. Shaw² | David Cobb² | Hailey M. Boone¹ | Roland Kays^{1,3} 

¹Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina, USA

²North Carolina Wildlife Resources Commission, Raleigh, North Carolina, USA

³North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA

Correspondence

Arielle W. Parsons
Email: aparsons@lpzoo.org

Present address

Arielle W. Parsons, Alexander Center for Applied Population Biology, Lincoln Park Zoo, Chicago, Illinois, USA.

Funding information

North Carolina Wildlife Resources Commission (Pittman-Robertson Wildlife Restoration Grant)

Handling Editor: Meredith K. Steele

Abstract

Predator–prey interactions are important for regulating populations and structuring communities but are affected by many dynamic, complex factors across large scales, making them difficult to study. Integrated population models (IPMs) offer a potential solution to understanding predator–prey relationships by providing a framework for leveraging many different datasets and testing hypotheses about interactive factors. Here, we evaluate the coyote–deer (*Canis latrans*–*Odocoileus virginianus*) predator–prey relationship across the state of North Carolina (NC). Because both species have similar habitat requirements and may respond to human disturbance, we considered net primary productivity (NPP) and urbanization as key mediating factors. We estimated deer survival and fecundity by integrating camera trap, harvest, and biological and hunter observation datasets into a two-stage, two-sex Lefkovich population projection matrix. We allowed survival and fecundity to vary as functions of urbanization, NPP, and coyote density, and projected abundance forward to test eight hypothetical scenarios. We estimated initial average deer and coyote densities to be 11.83 (95% CI: 5.64, 20.80) and 0.46 (95% CI: 0.02, 1.45) individuals/km², respectively. We found a negative, though highly uncertain, relationship between the current levels of coyote density and deer fecundity in most areas that became more negative under hypothetical conditions of lower NPP or higher urbanization, leading to lower projected deer abundances. Though not conclusive, our results indicate the possibility that coyotes could have stronger effects on deer populations in NC if their densities rise, but primarily in less productive and/or more suburban habitats. Our case study provides an example of how IPMs can be used to better understand the complex relationships between predator and prey under changing environmental conditions.

KEY WORDS

coyote, harvest data, integrated population model, net primary productivity, predator–prey interaction, urbanization, white-tailed deer

This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

INTRODUCTION

Interspecific interactions structure and shape wildlife communities (Elton, 1927). Predator-prey interactions are particularly important, with predators influencing prey reproductive success (Cherry et al., 2016), population growth rates (Pauliny et al., 2008), survival (Miller et al., 2006), and extinction risk (Owens & Bennett, 2000). However, interspecific interactions can also be altered via changes in the availability of anthropogenic resources (Hammond et al., 2020), hunting (Hoekstra & van den Bergh, 2005), and habitat (Kareiva, 1987), which may shift the balance between species. In particular, supplemental refuges (Berger, 2007) and/or food (Rodewald et al., 2011) can alter or decouple predator-prey relationships, leading to an overabundance of some species (Parsons et al., 2018) or increased risk of extinction for others (Newsome et al., 2015). Thus, identifying the potential consequences of human and environment-mediated changes to predator-prey dynamics is important to wildlife conservation and management.

Simple top-down or bottom-up approaches to modeling predator-prey relationships typically focus on the correlation of densities across space and time, but may be too simple to describe the more nuanced relationships that are likely important (i.e., effects of predation on recruitment) (McLennan et al., 1996). More complicated mechanistic models explore how abundance and demographic rates of prey are influenced by predators and environmental variables simultaneously, and are thus key for understanding predator-prey relationships (Hadjimichael et al., 2020). Common approaches involve classic population growth models (Messier, 1994) or matrix projection models (Nilsen et al., 2005), which can compare key natural (i.e., predator density, habitat, predation rates) and anthropogenic (e.g., disturbance, fragmentation, urbanization, hunting) factors impacting prey population dynamics. These models allow testing of outcomes from management interventions to inform decision-making (Martin et al., 2010), or produce predictions of animal responses to global change (Gilg et al., 2009). However, obtaining data to parameterize these models (i.e., estimates of abundance, survival, and fecundity) requires labor-intensive studies, which become more difficult as the geographic scope of inference increases. Fortunately, a flexible modeling framework, integrated population modeling (IPM; Schaub & Abadi, 2011), allows leveraging of many different datasets collected at different scales and provides formal accounting of uncertainty and enhanced precision, making IPMs an ideal tool for understanding the dynamics of interacting species at large scales (e.g., Elbroch et al., 2020).

One of the most studied mammals in North America is the white-tailed deer (*Odocoileus virginianus*; hereafter

“deer”), which ranges widely across the continent. Deer are managed by each state, typically informed by statewide harvest reports complimented with small-scale ancillary datasets like age distribution, litter size, and relative abundance. Together, these datasets can inform important aspects of deer ecology: hunting pressure, predation rates, human disturbance, and habitat quality. Deer hunting and vehicle collisions represent the two major sources of adult deer mortality in North America (Bowman et al., 2007), although hunting pressure has declined over the last several decades (Riley et al., 2003). Major predators of deer, particularly neonates, include black bears (*Ursus americanus*; Kautz et al., 2019), bobcats (*Lynx rufus*; Kautz et al., 2019), coyotes (*Canis latrans*; Kilgo et al., 2010), wolves (*Canis lupus*, *Canis rufus*; Olson et al., 2021), and cougars (*Puma concolor*), with the latter two being extirpated from most of the eastern portion of the white-tailed deer range. Because hunting is prohibited in most cities, and predator abundance is typically lower in developed areas, urbanization may create refuges where deer face lower predation rates (Berger, 2007). Landscaped yards and parks can also provide abundant forage, making suburban areas a high-quality deer habitat (Urbanek & Nielsen, 2013). Thus, we expect differences in deer reproduction, human disturbance, habitat, and predation rates to be interactive factors affecting deer abundance across large scales.

Here, we evaluate the interactive mediating factors of the coyote-deer predator-prey relationship across the state of North Carolina (NC). Coyote populations in NC have been increasing since the 1990s (Hody & Kays, 2018), and although little is known about their current dynamics, the population is thought to be below carrying capacity (DeBow et al., 1998; NCWRC, 2012a), and thus potentially still growing. Although many studies have established the ability of coyotes to negatively affect deer recruitment (Kilgo et al., 2012; Saalfeld & Ditchkoff, 2007; Watine & Giuliano, 2016), whether this impacts deer abundance is often less clear and subject to management intervention (i.e., doe harvest; Muthersbaugh, 2023) and the nuances of demographic and environmental factors (Kilgo et al., 2019). Urbanization and habitat fragmentation (Seto et al., 2012; Terando et al., 2014) are increasing in the region as is the effect of climate change with the potential to further affect habitat availability, primary productivity (Friend, 2010), and species interactions. Our goal is to build an IPM for deer using the best available data (e.g., camera traps, hunter observations, harvest data) to represent the relationship between deer demographic rates and three key dynamic and possibly interactive factors: coyote density, primary productivity, and urbanization. After establishing the current relationships, we will explore the potential consequences of

hypothetical increases or decreases in each factor on deer demographic rates and abundance. We hypothesize that at the current levels of coyote density, primary productivity, and urbanization, coyote density will have a negative relationship with deer recruitment. However, we hypothesize that despite an association with recruitment, coyote abundance will have little discernable relationship with deer abundance (e.g., Bragina et al., 2019). Nevertheless, we predict that if coyote density is hypothetically increased, we will reach a point where their impacts on deer abundance become important. We predict that this relationship will be most apparent in areas of low urbanization and/or low primary productivity, where resources are relatively scarce for both species.

MATERIALS AND METHODS

We used an IPM to explore the relationships between deer demographic rates and three key dynamic and interactive factors: coyote density, net primary productivity (hereafter NPP; Zhao & Running, 2010), and urbanization. We used the 2009 NPP derived by Zhao and Running (2010), which uses the global MODIS NPP algorithm (Running et al., 2004), to measure the rate at which solar energy is stored by plants as organic matter, with negative values indicating more decomposition than production. Here, we use NPP as a proxy for habitat quality, with higher NPP representing habitats with more available browse and cover for deer, both shown to affect survival rates of does and fawns (DePerno et al., 2000; Edge et al., 2023). Our IPM included two main components: (1) A vector of initial abundance estimates for each stage (fawns and adults) and sex, and (2) a projection matrix populated with survival probabilities and harvest rates for each stage and sex and a fecundity rate. We estimated initial abundances, survival, and fecundity using the best data available from several sources (see below). Deer are managed in NC across five deer management units (DMUs), which are delineated based on differences in population age structure and reproductive timing across the state (NCWRC, 2015). As the biology of the deer herd is known to vary across these DMUs, and ecological relationships for deer often vary across large spatial scales (Pease et al., 2022), we ran our model separately in each DMU to capture unmodeled sources of variation due to these factors. We allowed fecundity to vary as a function of urbanization, NPP, and coyote density to address our main hypothesis. Here, we describe the datasets and modeling approaches used (Figure 1), how we combined data likelihoods in an IPM framework, and how we used the model to make predictions about deer abundance under hypothetical scenarios of habitat, human

disturbance, and coyote density. As with any population model, our research is based on several assumptions, which we detail in Appendix S1: Table S1. Below, we give an overview of the methods, with more details provided in Appendix S2.

Initial deer abundance and coyote density

We used a subset of a statewide camera trap survey (Lasky et al., 2021), restricted by season and region (Appendix S2), to estimate the initial abundances of coyotes and deer. From July through December 2017, we worked with 37 trained volunteers to deploy 762 unbaited camera traps across NC (Appendix S1: Figure S1). Cameras were spaced >200 m and stratified randomly among forested, open ($>0.02 \text{ km}^2$ treeless), and developed habitat cover types proportional to their makeup within each county, as assessed with the US National Landcover Dataset (Dewitz, 2014). Although citizen science camera trap data tend to be opportunistic and thus prone to sampling bias (Weiser et al., 2020), they can be representative of large areas if sample size is high enough, as in the case of our dataset (Kays et al., 2021). Volunteers predominantly (~80%) used Reconyx (PC800, and PC900, Reconyx, Holmen, WI) with some (~15%) using Bushnell (Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS), (~3%) Browning (Strike Force, Browning Trail Cameras Birmingham, AL), and (~2%) Primos (Proof Cam 01, Primos Hunting Flora, MS). Trigger sensitivity was set to high for all cameras and we verified that all brands of cameras had similar trigger speeds (<0.5 s). Cameras were attached to trees at approximately 40 cm above the ground and deployed for 2–3 weeks before being moved to a new location. Cameras recorded three to five photographs per trigger, at a rate of 1 frame/s, re-triggering immediately if the animal was still in view. We grouped consecutive photos into sequences if they were <60 s apart, and used these sequences as independent records for doe, fawn, and coyote-abundance estimates (Kays et al., 2017). We binned captures into six monthly periods for the analysis.

We identified individual bucks based on their antler conformations (Parsons et al., 2017) and analyzed the resulting capture histories within a spatially explicit capture–recapture framework (hereafter SCR; Appendix S2; Royle et al., 2013). We were unable to individually identify coyotes or does on camera traps, and our cameras were spaced too far apart to use SCR on fawns; thus, we used camera trap detections and the spatial count model of Chandler and Royle (2013) (hereafter SCM) to estimate their abundances (Appendix S2).

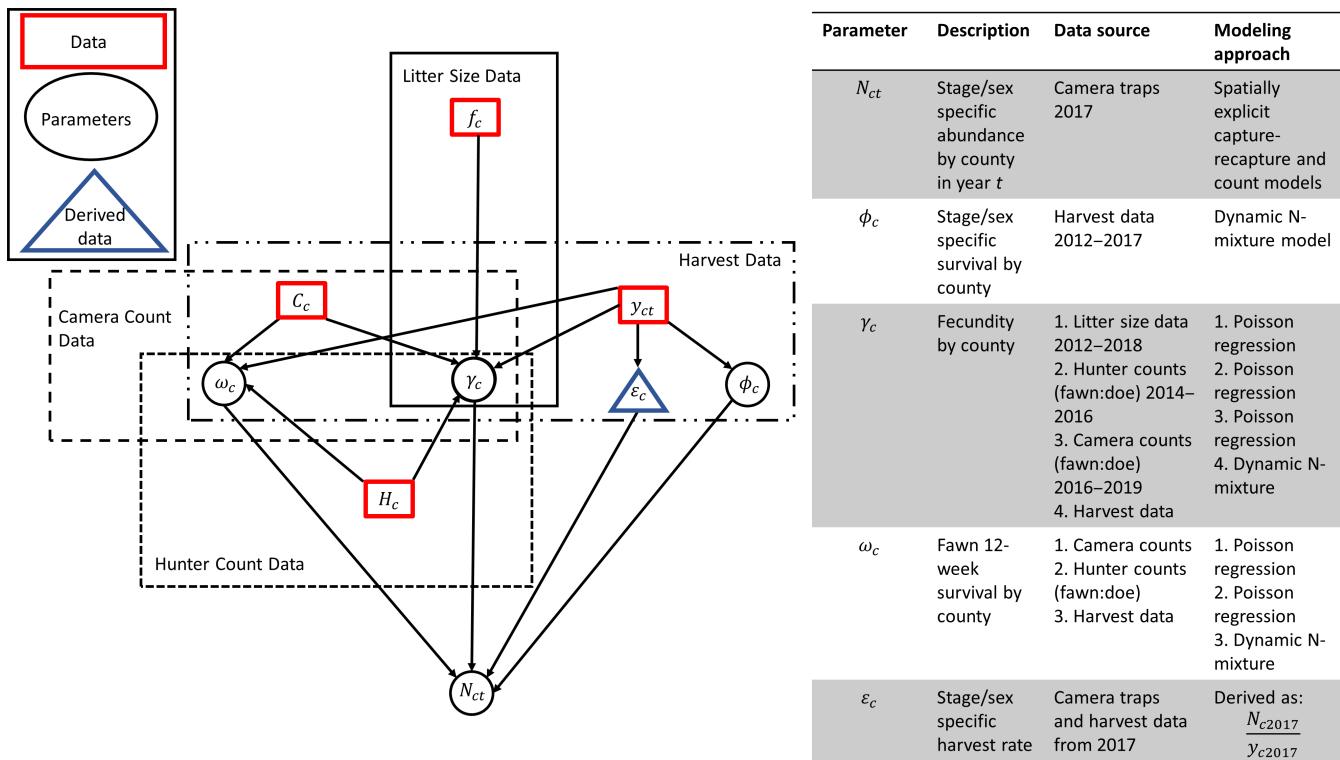


FIGURE 1 Integrated population model diagram highlighting the parameters, data sources, and modeling approaches used to estimate each element for the deer population in North Carolina. The fecundity parameter is shared between all datasets and represents those fawns that survive the risky first 12 weeks of life.

However, our camera spacing was large relative to fawn home range size, which can bias SCM model estimates (Chandler & Royle, 2013). We therefore conducted simulations to determine how much bias we might expect for our fawn abundance estimates to allow post hoc inflation of estimate uncertainty (Appendix S3). Due to the large spatial extent of our study (NC \sim 127,000 km 2), computation was challenging when running the entire state at once. Instead, we estimated abundance for 10 representative populations, two from each of the five DMUs of NC (Appendix S1: Figure S1). From these 10 populations, we quantified ecological relationships between landcover and abundance, using those relationships to predict abundance across the state as a function of forest cover (percent tree cover in a 1-km radius; Hansen et al., 2013), urbanization (percent developed land in a 1-km radius; Sohl et al., 2018), the interaction between the two and the proportion of hunted land in a 1-km radius (Burke et al., 2019). Although we were interested in how NPP mediates the interaction between coyote and deer, we did not use NPP in our initial abundance models, finding forest cover to be a stronger predictor of abundance in initial MLE count models (Akaike information criterion [AIC] Forest = 22,534, NPP = 22,558).

Deer fecundity

We defined fecundity as the number of fawns per doe that survived the first 12 weeks of life. We used hunter observations from three hunting seasons (2014–2016, each spanning September–January of the next year) and statewide camera trap data from 2016 to 2019, covering September–January of the next year (Lasky et al., 2021) to estimate the ratio of fawns to adult females (hereafter “does”; fawn:doe ratio) (see Appendix S2 and *Initial deer abundance and coyote density* for more details). We used deer fertility data to estimate litter size, which we adjusted for 12-week fawn survival using a prior with mean and variance taken from the literature (Appendix S1: Table S2, Appendix S2). The likelihoods of these three datasets were integrated together to provide more precise estimates of fecundity for our model and to represent fecundity from both hunted and unhunted populations (Zipkin & Saunders, 2018).

Fawn:doe ratio

To represent hunted populations, we used hunter observations from three hunting seasons (2014–2016, each

spanning September–January of the next year) from each county of NC. Hunters documented what species they observed and the number of hours they spent hunting, even if no species were observed, to get an index of abundance (Fuller et al., 2018). The location of these observations was known only at the county level. For use in our model, we removed all observations made over bait and averaged the observations of hunters that remained in the same hunting stand for multiple sessions. Our camera trap dataset indicated that does are less diurnal than fawns (does 42.15%, fawns 58.79%); thus, we corrected hunter observations (all diurnal) by multiplying doe counts by 1.394. We modeled the counts of does and fawns summed over all observers for the county as Poisson random variables with a mean intensity (i.e., intensity parameter). The intensity parameter associated with the count of fawns was parsed into three parameters representing the product of the intensity of does, litter size, and 12-week fawn survival.

To represent unhunted populations, we used statewide camera trap data from 2016 to 2019, covering September–January of the next year (Lasky et al., 2021), modeling the total count of does and fawns observed by camera traps in each county as Poisson random variables with a mean intensity. As we did for the hunted populations, we parsed the Poisson intensity parameter associated with the count of fawns into three parameters. The intensity of does parameter was unique to the camera trap and hunter observation datasets (i.e., separate parameters), while the litter size and 12-week fawn survival parameters were shared between the two data likelihoods. Because the parturition window typically closes between May and June (Chitwood et al., 2015; D’Angelo et al., 2005), fawns reach 12 weeks old approximately at the start of the hunting season in September, when data were collected. For both datasets, we modeled the intensity of does’ parameters as functions of average urbanization, average NPP, and average coyote density within each county (Appendix S2).

Litter size

We used the counts of fetuses collected from harvested does, vehicle collisions, and depredations to estimate litter size to provide additional information to estimate fecundity. Litter size data (number of fetuses/doe) are recorded by WRC staff in each county (99/100) each year for fertility data collection. Because within-year sample sizes were low, we used data from 2012 to 2018, modeling the average number of fetuses produced by each doe in each county as a Poisson random variable. Intensity was allowed to vary as a function of average urbanization,

average NPP, and average coyote density within each county (Appendix S2).

Deer survival and harvest rates

We used harvest data to estimate survival for adults of each sex and fawns. Deer harvests in NC are reported at the county level and distinguish between adult males (hereafter “bucks”), does, and button bucks (fawns). We used the dynamic N-mixture model of Zipkin et al. (2014) to estimate stage (fawns and adults) and sex-based survival outside of harvest seasons from stage-at-harvest data collected statewide from 2012 to 2017 over all 100 counties of NC (Appendix S2). We had to limit the number of predictors in this model to ensure convergence and chose two predictors likely to have the greatest impact on deer survival after the first 12 weeks of life: urbanization and the proportion of county area that allowed hunting. Furthermore, as all survival data came from hunted populations, but unhunted populations are likely to have higher survival, allowing county-level survival parameters to vary by the proportion of county area that allowed hunting was important to account for differences in deer survival across different landscapes (Etter et al., 2002). We estimated a mean harvest rate for 2017 outside of our model by dividing the stage-sex-specific harvest counts in each county by their respective county-level abundance estimates (see *Initial deer abundance and coyote density*) and allowed harvest rates in other years to vary around that mean (Appendix S2). Using the calculated harvest rates and estimated survival rates outside of the hunting season, we calculated an annual survival rate for each stage/sex to facilitate comparison with other studies. For adults, we multiplied the estimated survival rates outside of the hunting season (7 months; February–August) with the harvest rate (5 months; September–January). For fawns, we multiplied 12-week survival (3 months; June–August), harvest rate (5 months; September–January), and survival outside of the hunting season (4 months; February–May).

Population projections

Because we lacked age-specific deer abundance data (i.e., age [in years] determination not possible from camera traps), we used a stage-based model (2 stages: fawns and adult) in lieu of a more traditional age-based model. Using our model, we first established relationships between deer demographic rates (fecundity and stage/sex-specific survival) and our three covariates of interest (coyote density, NPP, and urbanization), allowing us to

simulate changes in demographic rates given changes in the covariates used to model them. We then ran eight hypothetical scenarios, varying coyote density (high = 0.8/km² and low = 0.2/km²), NPP (high = 2.0 and low = -2.0), and urbanization (high = 10% and low = 0% developed land in a 1-km radius) at different levels. Because urbanization is projected to increase across the southeastern United States in the coming decades (Terando et al., 2014), we tested scenarios to reflect an increase in the percent of urbanized landcover in each county, using the maximum percent observed (10%) as an upper bound compared with the minimum percent observed as a lower bound (0%; Table 1; Appendix S2). Similarly, as future increases in atmospheric CO₂ and associated changes in climate are expected to affect global patterns of plant production (Friend, 2010), we tested scenarios to reflect increases and decreases in NPP, using the upper and lower observed bounds in our dataset (high = 2.0 and low = -2.0 NPP; Table 1; Appendix S2). By varying each factor (coyote density, urbanization, and NPP), we assessed expected changes in fecundity, survival, population growth rate, and 10-year projected abundances in response to future extreme highs and lows in each factor.

Model fitting and evaluation

We fit our models in JAGS (Plummer, 2003) via the runjags (Denwood, 2016) interface in R (version 3.4.0, R Development Core Team, 2019) via R Studio (version 1.0.143, RStudio Team, 2015). We ran three chains, using trace plots, to determine an adequate burn-in phase, and subsequently continued running chains until the Brooks–Gelman–Rubin convergence diagnostic indicated adequate convergence (R-hat <1.1; Gelman et al., 2014). All models achieved adequate convergence by running for 200,000 iterations following a burn-in phase of 5000 iterations. Methods for assessing goodness-of-fit for IPMs have not been established, and although we did not formally assess the sensitivity of our results to the initial population structure due to computational limitations, we did formally evaluate the fit of each submodel using posterior-predictive checks (Appendix S2; Schaub & Abadi, 2011).

RESULTS

All submodels fit well with Bayesian *p* values $0.1 < p < 0.9$ except the doe and fawn initial abundance models for which *p* = 0, indicating poor model fit. This is not surprising given the large camera spacing relative to the expected

scale parameters, especially for fawns. Our simulations indicated that we could expect a 26% positive bias on our fawn abundance estimates using the SCM method due to large camera spacing (Appendix S3). To account for this, we added a 26% lower bound to our uncertainty estimate for initial fawn abundance in the fawn abundance submodel. Our density, survival, litter size, and fecundity estimates aligned well with other studies of deer and coyotes and tended to be more precise (Appendix S1: Table S2). Indeed, our estimates of doe annual survival and fawn 12-week survival were similar to estimates from a recent telemetry study in Cumberland County, NC, and more precise (Appendix S1: Table S3).

Initial abundance and covariate relationships

Over 13,313 trap nights at 851 camera sites over 100 counties, we detected coyotes on the camera traps 650 times and estimated the average coyote density in 2017 to be 0.46 (95% CI: 0.02, 1.45) individuals/km² (Appendix S1: Table S4). Coyote density was highest in the western third of NC (mountains) and in central NC in counties with high levels of urbanization (Figure 2). Indeed, our models estimated a positive, though weak (i.e., estimates overlapped zero), relationship between coyote density and urbanization for two ecoregions (coast and piedmont) and a weak negative relationship in the mountain ecoregion (at mean levels of forest cover, Appendix S1: Figure S2).

We captured bucks 4081 times, does 8642 times, and fawns 2009 times on our cameras. We identified 821 individual bucks an average of 1.7 times (SE = 0.05) each. The estimated statewide abundance of deer was 1.49 million (709,584, 2.62 million), corresponding to a deer density of 11.83 (95% CI: 5.64, 20.80) individuals/km², with the lowest densities occurring in the western part of the state and the highest densities occurring in counties with low levels of hunting and/or high levels of urbanization (Figure 2). The relationships between deer abundance and urbanization were uncertain, overlapping zero and varying by sex/stage and DMU. Buck abundance was positively associated with urbanization at mean levels of forest cover in DMU 1, while doe abundance was positively associated in DMUs 2 and 5, and fawn abundance was positively associated in DMUs 3 and 4. All other relationships between abundance and urbanization were negative or neutral (Appendix S1: Figure S2). The relationships between fawn abundance and urbanization at mean levels of forest generally mirrored the relationships between urbanization and either fawn survival outside of the hunting season or doe fecundity at mean coyote

TABLE 1 Hypothetical scenarios tested, varying levels of net primary productivity (NPP; county average), urbanization (percent urbanized land cover within the county), and coyote density (county average) for 100 counties in the state of North Carolina, USA.

Scenario	NPP level	Urbanization level	Coyote density
High NPP_High Coyote	2	Mean (4%)	0.8/km ²
Low NPP_High Coyote	-2	Mean (4%)	0.8/km ²
High NPP_Low Coyote	2	Mean (4%)	0.2/km ²
Low NPP_Low Coyote	-2	Mean (4%)	0.2/km ²
High Urbanization_High Coyote	Mean (0.15)	10%	0.8/km ²
Low Urbanization_High Coyote	Mean (0.15)	0%	0.8/km ²
High Urbanization_Low Coyote	Mean (0.15)	10%	0.2/km ²
Low Urbanization_Low Coyote	Mean (0.15)	0%	0.2/km ²

densities (Table 2). However, only coefficients associated with the relationship between urbanization and fawn abundance did not overlap zero (DMUs 1, 4, 5), with all other urbanization-related coefficients representing weak and uncertain relationships (Table 2; Appendix S1: Figure S2).

Harvest rate, survival, fecundity, and covariate relationships

Deer harvest rates for 2017 were highest in the central part of the state and lowest in the west and east, but varied by stage/sex. Buck harvest was typically higher, followed closely by doe harvest, with fawn harvest rates being lowest (Figure 2). Annual survival rates were high for adults of both sexes and low for fawns, impacted strongly by low 12-week fawn survival. All annual survival rates were highly variable, with no significant differences between DMUs (Appendix S1: Figure S3). Survival rates outside of the hunting season for all stages and sexes tended to be negatively associated with urbanization, though effect sizes were small and overlapped zero with only DMU 1, showing a consistent positive relationship (Appendix S1: Figure S2). Fecundity was highest in the central part of the state and lowest in the eastern and western regions (Figure 2). Deer fecundity was negatively related to coyote density at the mean levels of urbanization and NPP in 4/5 DMUs, but all estimates overlapped zero. The remaining DMU (DMU 3) showed a positive relationship between fecundity and coyote density and a strong positive relationship (i.e., estimate did not overlap zero) between fecundity and NPP when other factors were held at their means (Figure 3; Appendix S1: Figure S2). The relationship between deer fecundity and urbanization was negative or neutral for all DMUs when all other factors were held at their means except DMUs 3 and 5, with all estimates overlapping zero

(Appendix S1: Figure S2). Deer fecundity tended to be lowest at high coyote density and low NPP or urbanization; however, this trend was not statistically significant except in DMU 3 at intermediate levels of coyote density (Figure 4).

Demographic rates, population growth rates, and 10-year abundance projections under hypothetical scenarios

Using the current values of urbanization, NPP, and estimated coyote density for each DMU, we estimated the statewide white-tailed deer population growth rate to be 1.02 (95% CI: 1.01, 1.03), indicating a slightly increasing population (Appendix S1: Figure S4). We tested eight hypothetical scenarios of different levels of urbanization, NPP, and coyote density to simulate changes in fecundity, survival, and population growth rate over 10 years given the covariate relationships estimated by our model (Table 1).

At hypothetically high NPP (2.0), our model predicted a positive relationship between deer fecundity and coyote density (2/5 DMUs; DMUs 1, 4), which became negative at hypothetically low NPP (-2.0; Figure 4). At hypothetically high urbanization (10% in a 1-km radius), our model predicted a negative or neutral relationship between deer fecundity and coyote density (5/5 DMUs), which changed to a positive relationship at hypothetically low urbanization for some DMUs (0% in a 1-km radius; 2/5 DMUs, DMUs 1, 3; Figure 4). However, none of these differences were statistically significant. The only difference found that was statistically significant was in DMU 3, which exhibited a positive relationship between deer fecundity and coyote density at low NPP and a negative relationship at high NPP, with fecundity being significantly higher in high NPP at intermediate coyote density (Figure 4).

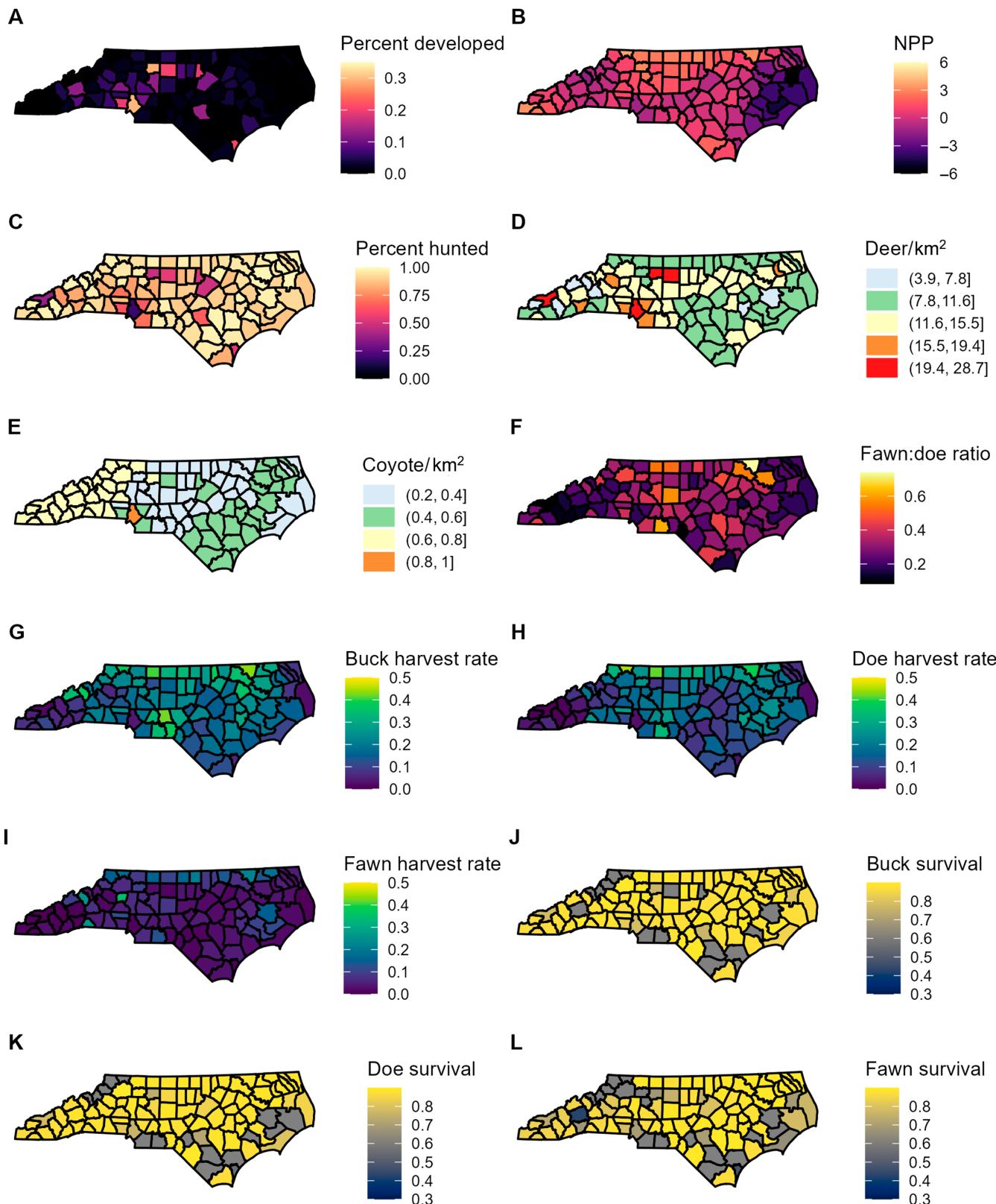


FIGURE 2 Statewide county-level results from integrated population model of deer in North Carolina. Covariates used in abundance modeling are: (A) average percent of each county that is developed, (B) average net primary productivity (NPP), and (C) average proportion of land that can be hunted in each county. We estimated the abundance of deer (D) and coyotes (E) from camera trap data and projected them across the state based on environmental relationships. We estimated fecundity (F) as the ratio of fawns:does. We estimated harvest rates (in percentage of county-level population harvested) and survival rates outside of the hunting season for bucks, does, and fawns (G–L, respectively).

TABLE 2 Summary of relationships (Appendix S1: Figure S2) with urbanization found for fawns in each deer management unit (DMU) of North Carolina.

DMU	Abundance	Fecundity	Survival February–May
1	– ^a	–	–
2	0	–	–
3	+	+	0
4	+ ^a	–	–
5	– ^a	+	0

Note: Abundance is the abundance of fawns immediately before they become adults. Fecundity represents the litter size of does in the DMU corrected for 12-week survival of neonate fawns. Survival is the survival of 8-month-old fawns (those that have survived from birth through the harvest) to the end of their first year. The + indicates a positive association with urbanization, – represents a negative association, and 0 represents no relationship.

^aCoefficient estimates that did not overlap zero. Relationships for abundance are shown at mean levels of forest cover for the DMU, and relationships for fecundity are shown at mean levels of coyote density for the DMU, with the relationship between urbanization and annual survival being independent of coyote density or forest cover.

When NPP and urbanization were held at 2017 levels, regardless of coyote density, our model predicted a declining population growth rate in 3/5 DMUs (DMUs

1, 4, 5), with the highest growth rates predicted when hypothetical coyote densities were lowest (Appendix S1: Figure S5). The only growing populations were projected in central DMUs 2 and 3, with the deer population predicted to grow in DMU 2 under low and moderate levels of hypothetical coyote density (0 and 0.5 coyotes/km², respectively) and in DMU 3 under the highest hypothetical level of coyote density (0.8/km²; Appendix S1: Figure S5). However, all projections were uncertain, with no statistical differences between projections at different levels of coyote density.

When urbanization was held at 2017 levels and NPP and coyote density allowed to vary between hypothetical levels, our model predicted higher projected relative deer abundances in scenarios where both NPP and coyote densities were at their highest for 3/5 DMUs (DMUs 1, 3, 4), and where NPP was high but coyote density low for the remaining DMUs (DMUs 2, 5; Figure 5). However, differences were not statistically significant. In scenarios where NPP was low, our model predicted higher or similar relative deer abundance where coyote density was also low (4/5 DMUs, DMUs 1, 2, 4, 5), though differences were not statistically significant, except in DMU 3 where hypothetically low NPP and high coyote density were

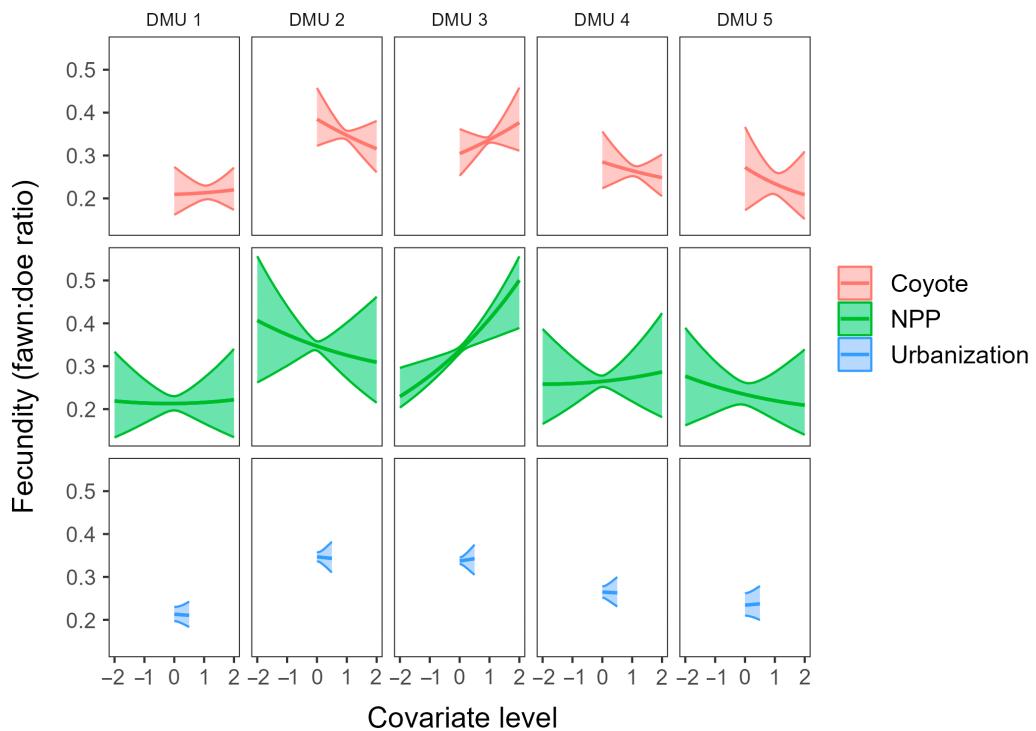


FIGURE 3 Relationships between three predictors and deer fecundity (fawn:doe ratio) when all other factors are held at their means. Covariate level refers to the value of each covariate, with coyote density ranging from 0.2 to 0.8 coyotes/km², net primary productivity (NPP) ranging from –2 to 2, and urbanization ranging from 0 to 1 representing 0% to 100% of land in a county being urbanized. Relationships are shown separately for each deer management unit (DMU) in the state of North Carolina. The relationship between coyote density and fecundity was generally negative while there were few strong relationships between NPP/urbanization and fecundity (Appendix S1: Figure S2).

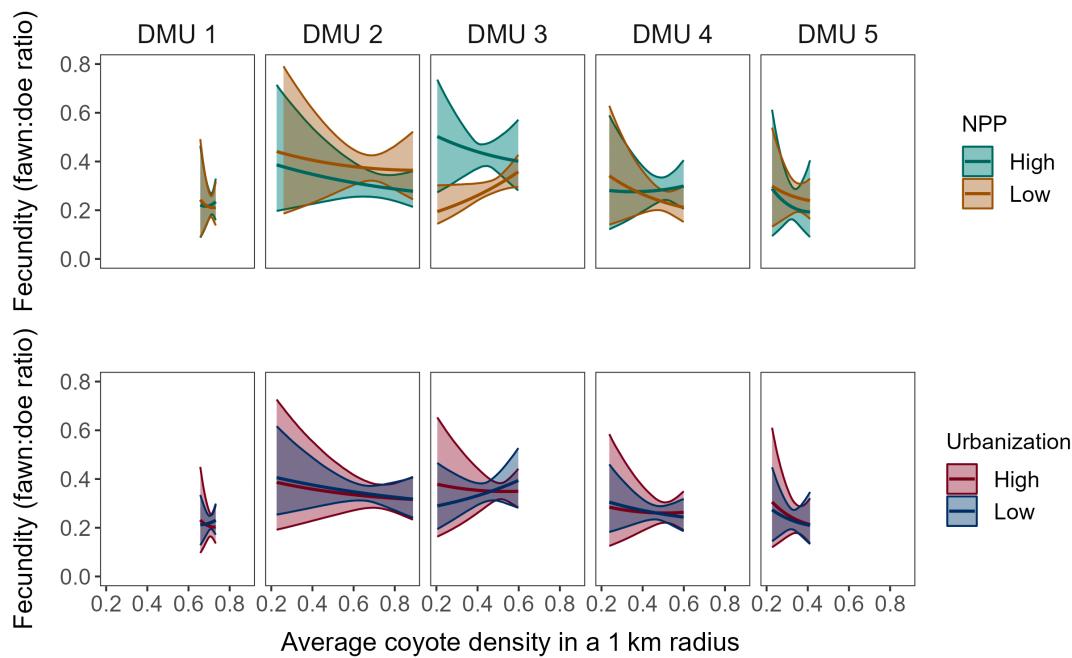


FIGURE 4 Relationship from an integrated population model between deer fecundity and coyote density at different hypothetical levels of urbanization (high = 10% of county urbanized, low = 0% of county urbanized) and net primary productivity (NPP; high = 2.0, low = -2.0) across the five deer management units (DMUs) of North Carolina. Fecundity tended to show a negative relationship with coyote density where NPP or urbanization was low. Higher levels of simulated NPP tended to lead to higher fecundity, especially where coyote densities were high. Uncertainty was high for all relationships.

associated with significantly higher deer abundance (Figure 5). DMU 3 was also the only DMU to exhibit a strong positive relationship between deer fecundity and coyote density and NPP, respectively, when other factors were held at their means (Figure 3). When NPP was held at 2017 levels and urbanization and coyote density were allowed to vary between hypothetical levels, our model predicted higher projected relative deer abundances in scenarios where coyote densities were low in DMUs 2, 4, and 5, regardless of urbanization level. This was most pronounced and consistent where urbanization was high, but only statistically different between the levels of coyote density at high urbanization in DMU 2 (Appendix S1: Figure S6).

DISCUSSION

This is the first study to analyze large-scale abundance and demographic rate estimates for mammal species within an IPM framework, incorporating predator-prey interactions, and habitat and human factors. Furthermore, our case study of deer and coyotes is the first published application of an IPM for deer in the United States (but see Messmer et al., 2020 from Canada). Our population modeling approach provides a more mechanistic understanding of predator-prey

relationships than is possible by linear models of predator and prey densities (e.g., Ponti et al., 2021). We tested predicted changes in deer abundance and demographic rates under eight hypothetical scenarios of varying levels of urbanization, primary productivity, and coyote density. Under our simulated conditions, we found evidence that high coyote densities are associated with lower deer fecundity, leading to lower abundance projections over time, with this negative association becoming stronger in counties with low NPP habitats and/or high levels of urbanization. However, the relationships we estimated and associated projections are uncertain, in part limited by the datasets available and the large-scale nature of our study. Nevertheless, our results illustrate how environmental conditions might interact with predator densities to potentially alter prey population dynamics and predator-prey relationships (e.g., Magle et al., 2014). We offer recommendations for future data collection to improve the accuracy, precision, and applicability of our model.

Parameter estimates

Our estimation of deer and coyote population metrics across large areas from camera traps is a new approach, and thus worth comparing our results with other studies

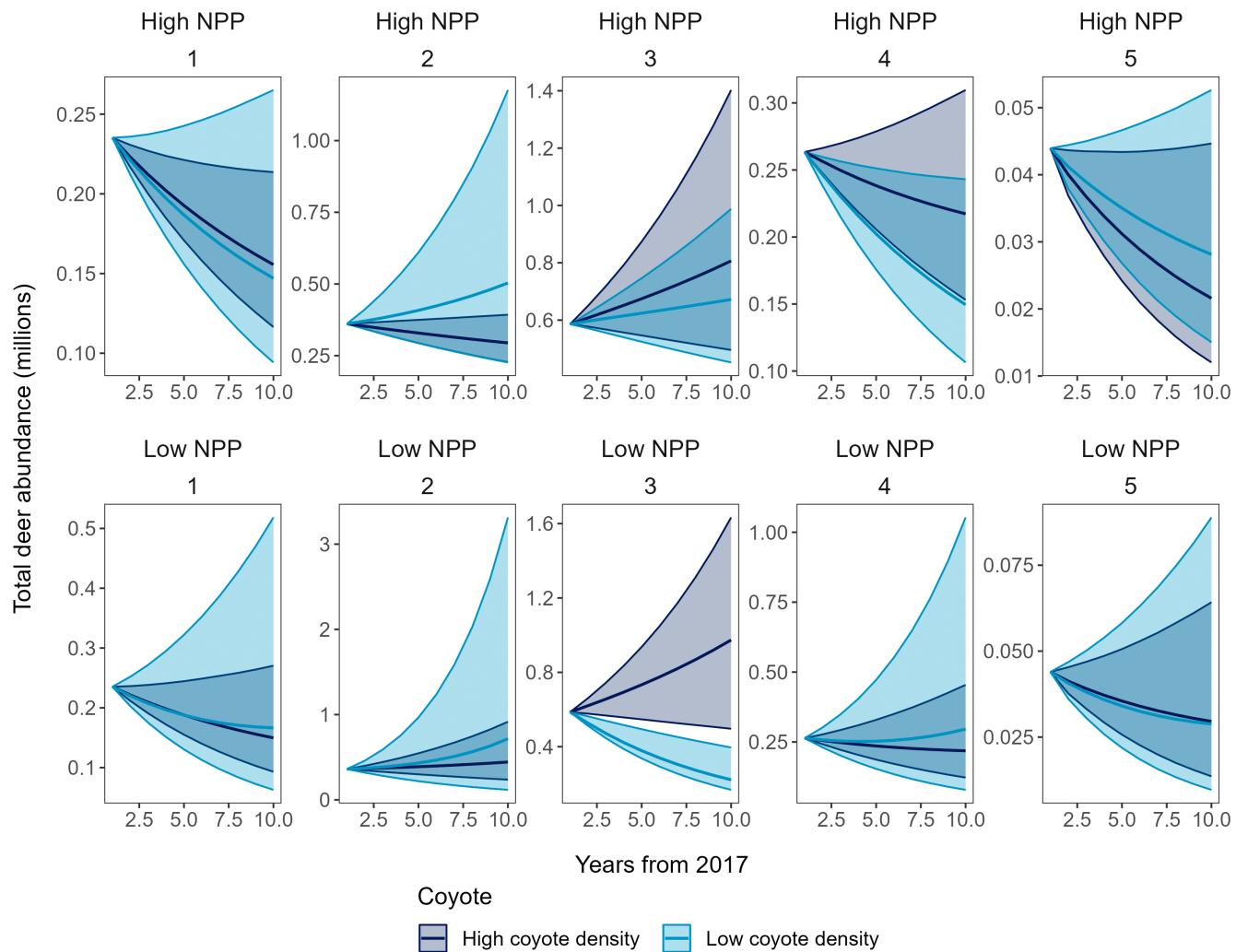


FIGURE 5 Deer abundance projections for the five deer management units (DMUs) of North Carolina for two hypothetical levels of coyote density (high = $0.8/\text{km}^2$, low = $0.2/\text{km}^2$) and net primary productivity (NPP; high = 2.0, low = -2.0). For each DMU, projections are based on an initial abundance for each sex/life stage (fawn, adult) multiplied through a Lefkovich matrix containing survival probabilities and harvest and fecundity rates. When coyote density was simulated high and NPP simulated low, this resulted in lower deer projected abundance for three of five DMUs. When both NPP and coyote densities were simulated high, this resulted in higher deer abundances for three of five DMUs.

(summarized in Appendix S1: Table S2). Despite the poor fit of doe and fawn models, our deer abundance estimates generated from camera trapping aligned well with estimates generated by the NCWRC from harvest data in terms of mapping similar patterns across the state and NCWRC density estimates falling within the 95% CI of our estimates. This indicates that cameras are a good complement to harvest data for monitoring deer, especially for suburban areas where harvest data are not available. Our coyote density estimates aligned well with other estimates from the southeast with similar means but had high uncertainty, suggesting that strategies such as targeted camera-trapping surveys to improve inference for coyotes should be further explored. Deer survival, litter size, and fecundity were similar to those reported by other studies from the region, often with greater or

similar precision, showing how commonly collected data requiring less effort (e.g., harvest data, camera survey counts) can yield similar results to more robust capture-recapture and/or telemetry data (Sollmann et al., 2013). Overall, this comparison of population parameters derived from our model with the range of values that might be expected based on previous research suggests that IPMs can be useful in providing meaningful estimates of key demographic factors for harvested populations across large scales.

Mediation of predator-prey relationships

The parameters estimated under our model are linked, with deer abundance being affected by demographic

rates, fecundity, and survival, which are themselves affected by outside factors such as harvest rates, habitat, and predation. We found that deer fecundity was negatively associated with coyote density across most of NC, but this relationship varied in magnitude across DMUs. Furthermore, when we allowed fecundity to vary with urbanization, NPP, and the interaction between those covariates and coyote density, we saw wider variation in relationships across the DMUs. We used DMU as a proxy to capture unknown sources of variation across different deer populations in the state, and the variable relationships that resulted illustrate the complex, interactive, dynamic relationship between coyotes and deer in NC. This dynamic relationship contrasts more static and predictable dynamics observed between deer and wolves and/or cougars in other parts of the country (Flagel et al., 2016; Kunkel & Pletscher, 1999; McKinney, 2001; Nelson & Mech, 1986), suggesting that the predator-prey relationship between deer and coyotes may be more dependent on local conditions. This might be expected because coyotes are much smaller than wolves and cougars, and are below the theoretical mass at which predators can specialize on large prey (Carbone et al., 1999). These condition-dependent predator-prey relationships might be more typical of a mesopredator taking advantage of abundant large prey when conditions are right than seen in apex predators.

Our hypothesis that, at the current conditions, coyote density has little discernable relationship with deer fecundity or abundance was partially supported. Although the relationships between deer fecundity and coyote density tended to be negative, they were not statistically different from zero. However, we noted variation in the relationship between deer fecundity and coyote density with urbanization and NPP. Although not significant at the current levels of coyote density, our results suggest that if NPP and/or urbanization in the region change over time, as expected, we might expect alterations in the dynamics between coyotes and deer.

Hypothetical scenarios to explore dynamics

Projecting population models under hypothetical conditions is common in ecology (e.g., population viability analysis; Akçakaya & Sjögren-Gulve, 2000), helping to identify key natural and anthropogenic factors impacting population dynamics and allowing the comparison of many alternate management or global change scenarios. While such comparisons can help better understand dynamics and evaluate the relative costs and benefits of possible management and conservation actions, because

future conditions are uncertain, model results are most appropriately compared relative to each other rather than considered as absolute predictions (McCarthy et al., 2003). Our scenario simulations allowed us to use the relationships we found in current populations to predict how this predator-prey dynamic might change under different scenarios. Given that coyote populations seem to be still increasing in the state (DeBow et al., 1998; NCWRC, 2012a), we explored how an increase in coyote density from 0.2 to 0.8 coyotes/km² would affect deer under different scenarios of NPP and urbanization.

Increasing coyote density at different levels of NPP

Our results suggest that higher coyote densities would be associated with reduced deer fecundity in some DMUs, but this depended on the NPP of an area. The association between coyote density and deer fecundity was most negative in areas of low productivity (NPP = 2.0) where high coyote densities would be most likely to limit deer populations. However, in more productive habitats, coyotes appear to have little impact on deer populations even at high densities. This supports our prediction that a negative association between coyote density and deer fecundity/abundance will be strongest in areas of low primary productivity, where resources are relatively scarce for both species. These results could be explained by deer benefiting from ample resources in productive habitats, resulting in better maternal health and/or higher reproductive rates (e.g., Aubin et al., 2022). If resources are high enough, this may also reduce predation pressure on fawns through prey switching by coyotes (Rodewald et al., 2011) or better fawn hiding strategies (Piccolo et al., 2010). However, fawn predation rates by coyotes even in productive habitats are generally high (Chitwood et al., 2015; Kilgo et al., 2012; Shuman et al., 2017) and prey switching may be less likely to favor relatively immobile and easy-to-catch neonates (Patterson et al., 1998), suggesting lower predation rates are less likely to explain lower coyote impacts in more productive habitats.

Increasing coyote density at different levels of urbanization

In contrast to NPP, higher levels of urbanization (high = 10%, low = 0%) were associated with lower deer fecundity and/or a negative relationship between coyote density and deer fecundity in most DMUs. This does not support our prediction that a negative association between coyote density and deer fecundity/abundance will be

strongest in areas of low urbanization and is inconsistent with the theory of prey using humans as shields to lower predation rates in urban areas (Berger, 2007) and/or changes in predator-hunting strategies (Haapakoski et al., 2013). Urban areas are associated with several factors that may affect species differently, depending on their level of adaptation, including human disturbance (Gallo et al., 2022), road networks (Riley et al., 2014), clumped and abundant resources (Andries et al., 2007), and habitat fragmentation (Gulsky et al., 2017; Parsons et al., 2022). Not accounting directly for these factors may have contributed to the overall variable and uncertain associations between deer fecundity and urbanization at mean levels of coyote density. Furthermore, we noted often strongly negative interaction terms between urbanization and forest cover in our density models, indicating habitat fragmentation, more than urbanization alone, is important to deer and coyotes. This might help explain why NPP was a stronger mediator of deer fecundity and coyote density than urbanization. Finally, despite the relatively high coyote densities we estimated in urbanized counties, predation rates, which we were unable to directly measure, may actually be lower in urban areas (i.e., Berger, 2007). Future research to examine coyote predation rates and hunting strategies in urban areas and explicit treatment of the predator-prey relationship (e.g., taking a Lotka-Volterra [Baker et al., 2017] or multimatrix approach [Barraquand & Gimenez, 2019]) within this modeling framework could improve our mechanistic understanding of this dynamic.

Model limitations and missing data

Our case study shows the potential for IPMs to estimate demographic rates and explore predator-prey dynamics under different hypothetical biological, global change, and management scenarios. The datasets we modeled included counts from camera traps, harvest, fecundity data, and hunter observations, all collected statewide. However, we lacked some data that would best inform key recruitment and harvest parameters, did not incorporate all sources of predation, and our data were not always representative of the entire statewide population. Below, we detail each of these areas where information is lacking and suggest ways in which they could be addressed to further develop this and similar models in a way that will be ideal for understanding complex, interactive, interspecific relationships.

Annual survival data for unharvested deer

We found a generally negative relationship between deer survival outside of the hunting season and

urbanization, which is inconsistent with past studies finding high survival in urban areas (McShea, 2012). Although this result may reflect increased mortality in suburban areas due to vehicle collisions (Etter et al., 2002), it is most likely because our survival data came exclusively from hunted populations, while most suburban populations are not hunted. We accounted for this by adding a correction factor, based on other survival studies in rural and developed areas, to adjust the county-wide survival rates as a function of the amount of huntale land in each county. A better solution would be to acquire new data on the survival of deer across different landscapes, hunted and unhunted, via robust design capture-recapture and/or telemetry. This would further improve our estimates of fawn annual survival, which tended to be lower and more uncertain than comparable studies.

Fawn 12-week survival

Fawns begin moving more widely after ~1 month and are most at risk of predation up until ~12 weeks of age (Kilgo et al., 2012). To use litter size data and camera/hunter counts of fawn:doe ratios simultaneously to estimate fecundity, litter size must be adjusted to account for 12-week survival. Because we lacked data to inform the estimation of 12-week survival, we used an informative prior in our model taken from the literature (Appendix S1: Table S2). Although 12-week survival was allowed to vary across counties within the bounds of our prior, unmodeled regional and local variation in 12-week survival could have strong impacts on scenario predictions. Traditionally, telemetry is the favored method for studying survival, but is challenging and often inaccurate for neonates (Murray, 2006). New developments like tight camera trap arrays with robust design of capture-recapture could offer economical alternatives (e.g., Chandler et al., 2018).

Bear and bobcat density across the state

To illustrate our case study, we kept our model simple by focusing on the interaction between coyotes and deer across NC. However, black bears and bobcats are both important predators of fawn neonates in NC (Boone, 2019; Shuman et al., 2017; Vreeland et al., 2004), and are heterogenous in their abundance across the state (Pease et al., 2022). Indeed, we found the lowest deer fecundity was in the western part of the state, which also has high black bear populations (NCWRC, 2012b). To improve the applicability of this model and our ability to understand the dynamic interactions of all species simultaneously,

black bears and bobcats should be explicitly added either in the same fashion as coyotes or using multiple interacting matrices (e.g., Barraquand & Gimenez, 2019).

Improved initial abundance estimates for does, fawns, and coyotes

Our initial abundance estimates for coyotes and does, for which we had no individual identification, were highly uncertain. Adding individual identifications and/or telemetry for a subset of animals could improve precision (i.e., via small-scale mark-resight efforts; Carter et al., 2019; Margenau et al., 2022). Although fawns were individually identifiable, the spacing of our cameras was too wide to obtain any recaptures across sites, prohibiting density estimation via traditional SCR. This could be improved using spaced grids of cameras. For example, Chandler et al. (2018) used 60 cameras with 250-m spacing to document 254 detections of 28 fawns over 7 months, allowing estimation of fawn density and survival. While repeating this level of effort on a statewide scale would be challenging, taking a representative population sampling approach (i.e., 2–3 camera grids in each DMU) and leveraging recent AI developments in individual identification (e.g., Miele et al., 2021) could increase the feasibility of such an undertaking.

Harvest and reporting rates

Our estimates of harvest rates (in percentage of total deer population harvested in each county) in 2017 were based on our abundance estimates (per stage and sex) and harvest counts. Thus, improving abundance estimates would also improve harvest rate estimates. Missing from our model is explicit modeling of spatiotemporal variation in harvest rates and an estimation of harvest reporting rates with associated uncertainty (Norton et al., 2012). Adding these features would be important to improving this model's relevance for management, both from the perspective of model realism and to allow exploration of the effects of manipulating harvest regulations on deer populations.

Conclusions

IPMs hold promise as a tool for better understanding the complex, interactive factors affecting the dynamics of interacting species and comparing management or conservation actions at a multispecies level. However, getting the diverse data needed at relevant scales can be challenging. We used three main strategies to scale up our

analysis while minimizing computation time and accounting for missing sources of data, which could be useful for similar projects: (1) use population subsets to establish relationships and predict across a larger region; (2) use different datasets where necessary to capture dynamics of interest (e.g., separate data for hunted and unhunted populations); (3) use values from the literature to capture phenomena known to affect dynamics but for which data are lacking. Although our results had high uncertainty and lacked broad statistical significance, our case study nevertheless indicates some support for a negative relationship between coyote density and deer fecundity, with evidence of NPP and/or urbanization having the potential to mediate this relationship. Despite a possible negative relationship between coyote density and deer fecundity, our results suggest little relationship between coyote density and deer abundance under current management at the current levels of coyote density, urbanization, and NPP in NC. When predators affect reproductive rates, this does not always result in numerical changes in prey population growth rates because other factors (i.e., age structure, sex ratio, adult, and juvenile survival) contribute to growth rate as well. However, our scenario simulation suggests that if NPP decreases due to climate change and/or urbanization in the region increases as predicted, coyotes could become a more important factor affecting deer populations. Thus, the relationships suggested by our analysis provide interesting foundational hypotheses on which to base future efforts. Overall, our model provides a framework to leverage disparate datasets, conferring the ability to better understand the complex relationships between predator and prey subject to changing environmental conditions.

ACKNOWLEDGMENTS

We would like to thank the staff of the NC Wildlife Resources Commission for data collection, data sharing, and assistance in camera trap data collection. We thank the citizen science volunteers, project interns, land managers, and librarians who made the camera trap survey possible. We thank M. Bogess for comments on an earlier version of this manuscript. We thank the NC Museum of Natural Sciences and NC State University for their continual support. Funding for this project was provided through a Pittman-Robertson Wildlife Restoration Grant and the NC Wildlife Resources Commission.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The camera trap data (Lasky et al., 2021) are available at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3372/>

suppinfo. The harvest, hunter observation, and litter size data (Parsons et al., 2024) are available from Dryad: <https://doi.org/doi:10.5061/dryad.h70rxwdpf>.

ORCID

Arielle W. Parsons  <https://orcid.org/0000-0003-1076-2896>

Roland Kays  <https://orcid.org/0000-0002-2947-6665>

REFERENCES

- Akçakaya, H. R., and P. Sjögren-Gulve. 2000. “Population Viability Analyses in Conservation Planning: An Overview.” *Ecological Bulletins* 48: 9–21.
- Anderies, J. M., M. Katti, and E. Shochat. 2007. “Living in the City: Resource Availability, Predation, and Bird Population Dynamics in Urban Areas.” *Journal of Theoretical Biology* 247: 36–49.
- Aubin, G. R., C. C. Nye, J. H. Rohm, R. T. Stamps, W. M. Ford, and M. J. Cherry. 2022. “Survival of White-Tailed Deer Fawns on Marine Corps Base Quantico.” *The Journal of Wildlife Management* 86: e22180.
- Baker, C. M., A. Gordon, and M. Bode. 2017. “Ensemble Ecosystem Modeling for Predicting Ecosystem Response to Predator Reintroduction.” *Conservation Biology* 31: 376–384.
- Barraquand, F., and O. Gimenez. 2019. “Integrating Multiple Data Sources to Fit Matrix Population Models for Interacting Species.” *Ecological Modelling* 411: 108713.
- Berger, J. 2007. “Fear, Human Shields and the Redistribution of Prey and Predators in Protected Areas.” *Biology Letters* 3: 620–23.
- Boone, H. M. 2019. *Estimating Abundance and Survival of White-Tailed Deer (*Odocoileus virginianus*) Fawns Using Camera Traps and Decoys*. Raleigh, NC: North Carolina State University.
- Bowman, J. L., H. A. Jacobson, D. S. Coggin, J. R. Heffelfinger, and B. D. Leopold. 2007. “Survival and Cause-Specific Mortality of Adult Male White-Tailed Deer Managed under the Quality Deer Management Paradigm.” *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 61: 76–81.
- Bragina, E. V., R. Kays, A. Hody, C. E. Moorman, C. S. Deperno, and L. S. Mills. 2019. “Effects on White-Tailed Deer Following Eastern Coyote Colonization.” *Journal of Wildlife Management* 83: 916–924.
- Burke, C. R., M. N. Peterson, D. T. Sawyer, C. E. Moorman, C. Serenari, and K. Pacifici. 2019. “A Method for Mapping Hunting Occurrence Using Publicly Available, Geographic Variables.” *Wildlife Society Bulletin* 43: 537–545.
- Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. “Energetic Constraints on the Diet of Terrestrial Carnivores.” *Nature* 402: 286–88.
- Carter, A., J. M. Potts, and D. A. Roshier. 2019. “Toward Reliable Population Density Estimates of Partially Marked Populations Using Spatially Explicit Mark–Resight Methods.” *Ecology and Evolution* 9: 2131–41.
- Chandler, R. B., K. Engebretsen, M. J. Cherry, E. P. Garrison, and K. V. Miller. 2018. “Estimating Recruitment from Capture–Recapture Data by Modelling Spatio-Temporal Variation in Birth and Age-Specific Survival Rates.” *Methods in Ecology and Evolution* 9: 2115–30.
- Chandler, R. B., and J. A. Royle. 2013. “Spatially Explicit Models for Inference about Density in Unmarked or Partially Marked Populations.” *The Annals of Applied Statistics* 7: 936–954.
- Cherry, M. J., K. E. Morgan, B. T. Rutledge, L. M. Conner, and R. J. Warren. 2016. “Can Coyote Predation Risk Induce Reproduction Suppression in White-Tailed Deer?” *Ecosphere* 7: e01481.
- Chitwood, M. C., M. A. Lashley, J. C. Kilgo, K. H. Pollock, C. E. Moorman, and C. S. Deperno. 2015. “Do Biological and Bedsite Characteristics Influence Survival of Neonatal White-Tailed Deer?” *PLoS One* 10: e0119070.
- D’Angelo, G. J., C. E. Comer, J. C. Kilgo, C. D. Drennan, D. A. Osborn, and K. V. Miller. 2005. “Daily Movements of Female White-Tailed Deer Relative to Parturition and Breeding.” In *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies*. 58 pp.
- DeBow, T. M., W. D. Webster, and P. W. Sumner. 1998. “Range Expansion of the Coyote, *Canis latrans* (Carnivora: Canidae), into North Carolina; with Comments on some Management Implications.” *Journal of the Elisha Mitchell Scientific Society* 114: 113–18.
- Denwood, M. J. 2016. “runjags: An R Package Providing Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS.” *Journal of Statistical Software* 71: 1–25.
- Deperno, C. S., J. A. Jenks, S. L. Griffin, and L. A. Rice. 2000. “Female Survival Rates in a Declining White-Tailed Deer Population.” *Wildlife Society Bulletin* 28: 1030–37.
- Dewitz, J. 2014. “National Land Cover Database (NLCD) 2011 Land Cover Conterminous United States [Data Set].” U.S. Geological Survey.
- Edge, A. C., J. P. Rosenberger, C. J. Yates, A. R. Little, C. H. Killmaster, K. L. Johannsen, D. A. Osborn, J. C. Kilgo, K. V. Miller, and G. J. D’Angelo. 2023. “White-Tailed Deer (*Odocoileus virginianus*) Fawn Survival and the Influence of Landscape Characteristics on Fawn Predation Risk in the Southern Appalachian Mountains, USA.” *PLoS One* 18: e0288449.
- Elbroch, L. M., J. M. Ferguson, H. Quigley, D. Craighead, D. J. Thompson, and H. U. Wittmer. 2020. “Reintroduced Wolves and Hunting Limit the Abundance of a Subordinate Apex Predator in a Multi-Use Landscape.” *Proceedings of the Royal Society B: Biological Sciences* 287: 20202202.
- Elton, C. 1927. *Animal Ecology*. London: Sidgwick and Jackson.
- Etter, D. R., K. M. Hollis, T. R. Van Deelen, D. R. Ludwig, J. E. Chelsvig, C. L. Anchor, and R. E. Warner. 2002. “Survival and Movements of White-Tailed Deer in Suburban Chicago, Illinois.” *The Journal of Wildlife Management* 66: 500–510.
- Flagel, D. G., G. E. Belovsky, and D. E. Beyer. 2016. “Natural and Experimental Tests of Trophic Cascades: Gray Wolves and White-Tailed Deer in a Great Lakes Forest.” *Oecologia* 180: 1183–94.
- Friend, A. D. 2010. “Terrestrial Plant Production and Climate Change.” *Journal of Experimental Botany* 61: 1293–1309.
- Fuller, J., C. Kreh, R. Myers, C. Olffenbuttel, J. Shaw, and A. Shipley. 2018. *Deer Hunter Observation Survey 2014–2018*. Raleigh, NC: North Carolina Wildlife Resources Commission.
- Gallo, T., M. Fidino, B. Gerber, A. A. Ahlers, J. L. Angstmann, M. Amaya, D. Drake, et al. 2022. “Mammals Adjust Diel Activity across Gradients of Urbanization.” *eLife* 11: e74756.

- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2014. *Bayesian Data Analysis*, 3rd ed. Boca Raton, FL: CRC Press.
- Gilg, O., B. Sittler, and I. Hanski. 2009. "Climate Change and Cyclic Predator–Prey Population Dynamics in the High Arctic." *Global Change Biology* 15: 2634–52.
- Gulsby, W. D., J. C. Kilgo, M. Vukovich, and J. A. Martin. 2017. "Landscape Heterogeneity Reduces Coyote Predation on White-Tailed Deer Fawns." *The Journal of Wildlife Management* 81: 601–9.
- Haapakoski, M., J. Sundell, and H. Ylönen. 2013. "Mammalian Predator–Prey Interaction in a Fragmented Landscape: Weasels and Voles." *Oecologia* 173: 1227–35.
- Hadjimichael, A., P. M. Reed, and J. D. Quinn. 2020. "Navigating Deeply Uncertain Tradeoffs in Harvested Predator–Prey Systems." *Complexity* 5: 1–19.
- Hammond, T. T., C. A. Ortiz-Jimenez, and J. E. Smith. 2020. "Anthropogenic Change Alters Ecological Relationships Via Interactive Changes in Stress Physiology and Behavior within and among Organisms." *Integrative and Comparative Biology* 60: 57–69.
- Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, et al. 2013. "High-Resolution Global Maps of 21st-Century Forest Cover Change." *Science* 342: 850–53.
- Hody, J. W., and R. Kays. 2018. "Mapping the Expansion of Coyotes (*Canis latrans*) across North and Central America." *ZooKeys* 759: 81–97.
- Hoekstra, J., and J. C. van den Bergh. 2005. "Harvesting and Conservation in a Predator–Prey System." *Journal of Economic Dynamics and Control* 29: 1097–1120.
- Kareiva, P. 1987. "Habitat Fragmentation and the Stability of Predator–Prey Interactions." *Nature* 326: 388–390.
- Kautz, T. M., J. L. Belant, D. E. Beyer, Jr., B. K. Strickland, T. R. Petreolje, and R. Sollmann. 2019. "Predator Densities and White-Tailed Deer Fawn Survival." *The Journal of Wildlife Management* 83: 1261–70.
- Kays, R., M. Lasky, A. W. Parsons, B. Pease, and K. Pacifici. 2021. "Evaluation of the Spatial Biases and Sample Size of a Statewide Citizen Science Project." *Citizen Science Theory and Practice* 6: 34.
- Kays, R., A. W. Parsons, M. C. Baker, E. L. Kalies, T. Forrester, R. Costello, C. T. Rota, J. J. Millspaugh, and W. J. McShea. 2017. "Does Hunting or Hiking Affect Wildlife Communities in Protected Areas?" *Journal of Applied Ecology* 54: 242–252.
- Kilgo, J. C., M. J. Cherry, S. S. Ditchkoff, W. D. Gulsby, and K. V. Miller. 2019. "Coyotes and White-Tailed Deer Populations in the East." *The Journal of Wildlife Management* 83: 1636–40.
- Kilgo, J. C., H. S. Ray, C. Ruth, and K. V. Miller. 2010. "Can Coyotes Affect Deer Populations in Southeastern North America?" *The Journal of Wildlife Management* 74: 929–933.
- 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." *The Journal of Wildlife Management* 76: 1420–30.
- Kunkel, K., and D. H. Pletscher. 1999. "Species-Specific Population Dynamics of Cervids in a Multipredator Ecosystem." *The Journal of Wildlife Management* 63: 1082–93.
- Lasky, M., A. W. Parsons, S. G. Schuttler, G. Hess, R. Sutherland, L. Kalies, S. Clark, et al. 2021. "Carolina Critters: A Collection of Camera-Trap Data from Wildlife Surveys across North Carolina." *Ecology* 102: e03372.
- Magle, S. B., L. S. Simoni, E. W. Lehrer, and J. S. Brown. 2014. "Urban Predator–Prey Association: Coyote and Deer Distributions in the Chicago Metropolitan Area." *Urban Ecosystems* 17: 875–891.
- Margenau, L. L., M. J. Cherry, K. V. Miller, E. P. Garrison, and R. B. Chandler. 2022. "Monitoring Partially Marked Populations Using Camera and Telemetry Data." *Ecological Applications* 32: e2553.
- Martin, J., A. F. O'Connell, Jr., W. L. Kendall, M. C. Runge, T. R. Simons, A. H. Waldstein, S. A. Schulte, et al. 2010. "Optimal Control of Native Predators." *Biological Conservation* 143: 1751–58.
- McCarthy, M. A., S. J. Andelman, and H. P. Possingham. 2003. "Reliability of Relative Predictions in Population Viability Analysis." *Conservation Biology* 17: 982–89.
- McKinney, B. P. 2001. *Mountain Lions, Deer, and Predator Control* 70–73. Kerrville, TX: Texas Agricultural Research and Extension Center.
- McLennan, J. A., M. A. Potter, H. A. Robertson, G. C. Wake, R. Colbourne, L. Dew, L. Joyce, et al. 1996. "Role of Predation in the Decline of Kiwi, *Apteryx* spp., in New Zealand." *New Zealand Journal of Ecology* 20: 27–35.
- McShea, W. J. 2012. "Ecology and Management of White-Tailed Deer in a Changing World." *Annals of the New York Academy of Sciences* 1249: 45–56.
- Messier, F. 1994. "Ungulate Population Models with Predation: A Case Study with the North American Moose." *Ecology* 75: 478–488.
- Messmer, D. J., A. E. Henderson, T. M. Whiklo, and K. R. Conkin. 2020. "Integrated Population Modeling for White-Tailed Deer in Saskatchewan, Canada." *The Journal of Wildlife Management* 84: 1224–33.
- Miele, V., G. Dussert, B. Spataro, S. Chamaillé-Jammes, D. Allainé, and C. Bonenfant. 2021. "Revisiting Animal Photo-Identification Using Deep Metric Learning and Network Analysis." *Methods in Ecology and Evolution* 12: 863–873.
- Miller, D. A., J. B. Grand, T. F. Fondell, and M. Anthony. 2006. "Predator Functional Response and Prey Survival: Direct and Indirect Interactions Affecting a Marked Prey Population." *Journal of Animal Ecology* 75: 101–110.
- Murray, D. L. 2006. "On Improving Telemetry-Based Survival Estimation." *The Journal of Wildlife Management* 70: 1530–43.
- Muthersbaugh, M. 2023. *Drivers of White-Tailed Deer (*Odocoileus virginianus*) Behavior, Survival, and Population Growth in the Piedmont of South Carolina*. Clemson, SC: Clemson University.
- NCWRC. 2012a. *Fox and Coyote Populations Study Final Report*. Raleigh, NC: North Carolina Wildlife Resources Commission.
- NCWRC. 2012b. *North Carolina Black Bear Management Plan 2012–2022*. Raleigh, NC: North Carolina Wildlife Resources Commission.
- NCWRC. 2015. *Evaluation of Deer Hunting Season Structures and Deer Management Units in North Carolina*. Raleigh, NC: North Carolina Wildlife Resources Commission.
- Nelson, M. E., and L. D. Mech. 1986. "Mortality of White-Tailed Deer in Northeastern Minnesota." *Journal of Wildlife Management* 50: 691–98.
- Newsome, T. M., J. A. Dellinger, C. R. Pavey, W. J. Ripple, C. R. Shores, A. J. Wirsing, and C. R. Dickman. 2015. "The

- Ecological Effects of Providing Resource Subsidies to Predators.” *Global Ecology and Biogeography* 24: 1–11.
- Nilsen, E. B., T. Pettersen, H. Gundersen, J. M. Milner, A. Mysterud, E. J. Solberg, H. P. Andreassen, and N. C. Stenseth. 2005. “Moose Harvesting Strategies in the Presence of Wolves.” *Journal of Applied Ecology* 42: 389–399.
- Norton, A. S., D. R. Diefenbach, B. D. Wallingford, and C. S. Rosenberry. 2012. “Spatio-Temporal Variation in Male White-Tailed Deer Harvest Rates in Pennsylvania: Implications for Estimating Abundance.” *The Journal of Wildlife Management* 76: 136–143.
- Olson, L. O., T. R. Van Deelen, D. J. Storm, and S. M. Crimmins. 2021. “Understanding Environmental Patterns of Canid Predation on White-Tailed Deer (*Odocoileus virginianus*).” *Canadian Journal of Zoology* 99: 912–920.
- Owens, I. P., and P. M. Bennett. 2000. “Ecological Basis of Extinction Risk in Birds: Habitat Loss Versus Human Persecution and Introduced Predators.” *Proceedings of the National Academy of Sciences of the United States of America* 97: 12144–48.
- Parsons, A., K. Pacifici, J. Shaw, D. Cobb, H. Boone, and R. Kays. 2024. “Data From: Urbanization and Primary Productivity Mediate the Predator-Prey Relationship between Deer and Coyotes.” Dataset. Dryad. <https://doi.org/10.5061/dryad.h70rxwdpf>.
- Parsons, A. W., T. Forrester, M. C. Baker-Whatton, W. J. McShea, C. T. Rota, S. G. Schuttler, J. J. Millspaugh, and R. Kays. 2018. “Mammal Communities Are Larger and More Diverse in Moderately Developed Areas.” *eLife* 7: e38012.
- Parsons, A. W., T. Forrester, W. J. McShea, M. C. Baker-Whatton, J. J. Millspaugh, and R. Kays. 2017. “Do Occupancy or Detection Rates from Camera Traps Reflect Deer Density?” *Journal of Mammalogy* 98: 1547–57.
- Parsons, A. W., K. F. Kellner, C. T. Rota, S. G. Schuttler, J. J. Millspaugh, and R. W. Kays. 2022. “The Effect of Urbanization on Spatiotemporal Interactions between Gray Foxes and Coyotes.” *Ecosphere* 13: e3993.
- Patterson, B., L. Benjamin, and F. Messier. 1998. “Prey Switching and Feeding Habits of Eastern Coyotes in Relation to Snowshoe Hare and White-Tailed Deer Densities.” *Canadian Journal of Zoology* 76: 1885–97.
- Pauliny, A., M. Larsson, and D. Blomqvist. 2008. “Nest Predation Management: Effects on Reproductive Success in Endangered Shorebirds.” *The Journal of Wildlife Management* 72: 1579–83.
- Pease, B. S., K. Pacifici, and R. Kays. 2022. “Exploring Spatial Nonstationarity for Four Mammal Species Reveals Regional Variation in Environmental Relationships.” *Ecosphere* 13: e4166.
- Piccolo, B. P., T. R. Van Deelen, K. Hollis-Etter, D. R. Etter, R. E. Warner, and C. Anchor. 2010. “Behavior and Survival of White-Tailed Deer Neonates in Two Suburban Forest Preserves.” *Canadian Journal of Zoology* 88: 487–495.
- Plummer, M. 2003. “JAGS: A Program for Analysis of Bayesian Graphical Models using Gibbs Sampling.” In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, pp. 1–10.
- Ponti, L., A. P. Gutierrez, M. R. de Campos, N. Desneux, A. Biondi, and M. Neteler. 2021. “Biological Invasion Risk Assessment of *Tuta Absoluta*: Mechanistic Versus Correlative Methods.” *Biological Invasions* 23: 3809–29.
- R Development Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Riley, S. J., D. J. Decker, J. W. Enck, P. D. Curtis, T. B. Lauber, and T. L. Brown. 2003. “Deer Populations Up, Hunter Populations Down: Implications of Interdependence of Deer and Hunter Population Dynamics on Management.” *Ecoscience* 10: 455–461.
- Riley, S. P., J. L. Brown, J. A. Sikich, C. M. Schoonmaker, and E. E. Boydston. 2014. *Wildlife Friendly Roads: The Impacts of Roads on Wildlife in Urban Areas and Potential Remedies* 323–360. Boston, MA: Urban Wildlife Conservation, Springer.
- Rodewald, A. D., L. J. Kearns, and D. P. Shustack. 2011. “Anthropogenic Resource Subsidies Decouple Predator-Prey Relationships.” *Ecological Applications* 21: 936–943.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. *Spatial Capture-Recapture*. Waltham, MA: Academic Press.
- RStudio Team. 2015. *RStudio: Integrated Development for R*. Boston, MA: RStudio, Inc.
- Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto. 2004. “A Continuous Satellite-Derived Measure of Global Terrestrial Primary Production.” *BioScience* 54: 547–560.
- Saalfeld, S. T., and S. S. Ditchkoff. 2007. “Survival of Neonatal White-Tailed Deer in an Exurban Population.” *The Journal of Wildlife Management* 71: 940–44.
- Schaub, M., and F. Abadi. 2011. “Integrated Population Models: A Novel Analysis Framework for Deeper Insights into Population Dynamics.” *Journal of Ornithology* 152: 227–237.
- Seto, K. C., B. Güneralp, and L. R. Hutyra. 2012. “Global Forecasts of Urban Expansion to 2030 and Direct Impacts on Biodiversity and Carbon Pools.” *Proceedings of the National Academy of Sciences of the United States of America* 109: 16083–88.
- Shuman, R. M., M. J. Cherry, T. N. Simoneaux, E. A. Dutoit, J. C. Kilgo, M. J. Chamberlain, and K. V. Miller. 2017. “Survival of White-Tailed Deer Neonates in Louisiana.” *The Journal of Wildlife Management* 81: 834–845.
- Sohl, T. L., K. L. Sayler, M. A. Bouchard, R. R. Reker, A. M. Freisz, S. L. Bennett, B. M. Sleeter, et al. 2018. *Conterminous United States Land Cover Projections – 1992 to 2100*. Sioux Falls, SD: USGS EROS Center.
- Sollmann, R., A. Mohamed, H. Samejima, and A. Wilting. 2013. “Risky Business or Simple Solution—Relative Abundance Indices from Camera-Trapping.” *Biological Conservation* 159: 405–412.
- Terando, A. J., J. Costanza, C. Belyea, R. R. Dunn, A. McKerrow, and J. A. Collazo. 2014. “The Southern Megalopolis: Using the Past to Predict the Future of Urban Sprawl in the Southeast U.S.” *PLoS One* 9: 1–8.
- Urbanek, R. E., and C. K. Nielsen. 2013. “Influence of Landscape Factors on Density of Suburban White-Tailed Deer.” *Landscape and Urban Planning* 114: 28–36.
- 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.

- Watine, L. N., and W. M. Giuliano. 2016. "Coyote Predation Effects on White-Tailed Deer Fawns." *Natural Resources* 7: 628–643.
- Weiser, E. L., J. E. Diffendorfer, L. Lopez-Hoffman, D. Semmens, and W. E. Thogmartin. 2020. "Challenges for Leveraging Citizen Science to Support Statistically Robust Monitoring Programs." *Biological Conservation* 242: 108411.
- Zhao, M., and S. W. Running. 2010. "Drought-Induced Reduction in Global Terrestrial Net Primary Production from 2000 through 2009." *Science* 329: 940–43.
- Zipkin, E. F., and S. P. Saunders. 2018. "Synthesizing Multiple Data Types for Biological Conservation Using Integrated Population Models." *Biological Conservation* 217: 240–250.
- Zipkin, E. F., J. T. Thorson, K. See, H. J. Lynch, E. H. C. Grant, Y. Kanno, R. B. Chandler, B. H. Letcher, and J. A. Royle. 2014. "Modeling Structured Population Dynamics Using Data from Unmarked Individuals." *Ecology* 95: 22–29.

SUPPORTING INFORMATION

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

How to cite this article: Parsons, Arielle W., Krishna Pacifici, Jonathan C. Shaw, David Cobb, Hailey M. Boone, and Roland Kays. 2024. "Urbanization and Primary Productivity Mediate the Predator–Prey Relationship between Deer and Coyotes." *Ecosphere* 15(6): e4882. <https://doi.org/10.1002/ecs2.4882>