Evidence of reduced abundance, density, and survival of coyotes under federal management for red wolf recovery

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Abstract

To mitigate coyote (*Canis latrans*) introgression in the wild red wolf (*Canis rufus*) genome, the United States Fish and Wildlife Service (USFWS) Red Wolf Recovery Program used a combination of reproductive sterilization and lethal removal of coyotes to minimize hybridization and increase the endangered red wolf population. Although sterilization assisted in limiting coyote introgression to ≤4% in the wild red wolf genome, its potential negative effect on coyote and hybrid abundance and density is unknown. Using long-term capture–mark–recapture and radio-telemetry data collected on red wolves, coyotes, and hybrids under the USFWS Red Wolf Adaptive Management Plan implemented during 2000–2013, we explored three areas of research: (1) spatial modeling to correlate land cover characteristics with the relative probabilities of capture for red wolves, coyotes, and hybrids; (2) survival analysis of radio-marked canids; and (3) annual population estimates for the three *Canis* taxa. We detected no differences in the relative probability of capture among *Canis* taxa. Red wolves, coyotes, and hybrids were most frequently captured in areas proximate to road networks with low canopy cover (i.e., cropland) and away from coastal bottomland forests. Annual apparent survival for red wolves and hybrids was greater than survival for coyotes; however, wolves and hybrids exhibited similar annual survival. Mortality of coyotes and hybrids was predominately attributed to deliberate take through lethal control by the USFWS biologists and harvest by hunters and trappers. We observed annual densities of coyotes ranging between 2.5 and 21.5 coyotes/1000 km^2, with densities annually increasing during 2005–2013 when the red wolf population plateaued before declining after 2013. Despite the increase in coyote density, our density estimates are less than most estimates reported throughout the coyote's geographic range, and similar to those reported in areas where coyote populations are limited by extreme environments such as their northern range limits in Alaska, United States, and Canada. Our findings indicate that red wolf presence and federal management

of coyotes using fertility control may have limited coyote densities in north-eastern North Carolina.

KEYWORDS

Canis latrans, *Canis rufus*, carnivore management, conservation, long-term monitoring, nonlethal control, red wolf recovery, sterilization

INTRODUCTION

Throughout North America, coyotes (*Canis latrans*) exist along rural-to-urban gradients and exhibit considerable adaptability to human presence. Management of coyotes along this gradient is complex and controversial, as resource managers implement a variety of lethal and nonlethal methods to mitigate coyote–human conflicts (Knowlton et al., 1985; Mitchell et al., 2004; Shivik, 2004). However, coyote populations are resilient to lethal management in ways that other *Canis* populations, such as gray wolves (*Canis lupus*), eastern wolves (*Canis lycaon*), and red wolves (*Canis rufus*), are not. This resiliency is self-evident by the fact that wolf populations in the United States required reintroduction projects (Hinton et al., 2013; Parsons, 1998; Smith et al., 2003), legal protection (Bruskotter et al., 2011, 2014; Carroll et al., 2010), and ongoing management (Berry et al., 2016; Hinton, Rabon, & Chamberlain, 2015; Way & Bruskotter, 2012) to persist, whereas coyotes expanded their geographic range while being aggressively targeted by government-sponsored eradication programs (Bergstrom et al., 2014; LeSher, 2020; Murphy, 2020; Nunley, 1985, 2004). The mechanisms by which coyotes overcome lethal management are not well known, but research has suggested that compensatory breeding (Conner et al., 1998; Connolly & Longhurst, 1975; Sterling et al., 1983) and immigration (Conner et al., 1998; Kierepka et al., 2017; Kilgo et al., 2017) are likely causal.

Previous studies reported that lethal strategies to control coyote populations often fail because resident breeding pairs are resistant to nonselective removal techniques (Bromley & Gese, 2001a; Conner et al., 2008; Jaeger et al., 2001; Sacks et al., 1999), prompting management strategies that focus on specific classes of animals (Bromley & Gese, 2001a, 2001b; Seidler & Gese, 2012; Till & Knowlton, 1983). Specifically, reproductive sterilization of resident coyotes has been used under the assumption that provisioning offspring is energetically costly, and in the absence of offspring, residents are less likely to target larger prey if they do not need to provision for pups (Bromley & Gese, 2001a, 2001b; Seidler et al., 2014). Management implications of sterilizing coyotes have been evaluated with the intent to mitigate coyote depredation on livestock (Bromley & Gese, 2001a) and game species (Seidler et al., 2014). For example, Seidler et al. (2014) reported that sterilized resident coyotes were less likely to prey on pronghorn antelope (*Antilocapra americana*) than were non-sterile residents with offspring. At a larger scale, sterilization was adopted as a centerpiece to the United States Fish and Wildlife Service (USFWS) Red Wolf Adaptive Management Plan (RWAMP) and implemented across a 6000-km^2 region of northeastern North Carolina to reduce hybridization between red wolves and coyotes (Gese & Terletzky, 2015; Kelly, 2000).

The use of sterilization to limit hybridization between coyotes and red wolves is commonly noted in studies (e.g., Brzeski et al., 2014; Gese et al., 2015; Hinton et al., 2018; Hinton & Chamberlain, 2014) and was evaluated by Gese and Terletzky (2015). In their assessment, Gese and Terletzky (2015) introduced the "placeholder" concept of using sterile coyotes and red wolf–coyote hybrids (hereafter, "hybrids") to reduce genetic introgression in the reintroduced red wolf population, and reported that placeholders routinely held territories, had greater survival rates than red wolves, and approximately 37% of placeholders were displaced by wolves. The underlying tenet of the placeholder concept was that space was limiting and all suitable space in the Red Wolf Experimental Population Area (hereafter, "NC Recovery Area") should be occupied by breeding wolf pairs and, where wolf pairs were absent, space should be occupied by placeholders (Kelly, 2000; Rabon et al., 2013). As red wolf numbers increased, placeholder territories would be usurped for red wolves either by the wolves themselves through interspecific strife or by the USFWS Red Wolf Recovery Program (hereafter, "Recovery Program") biologists removing placeholders to create vacancies for dispersing wolves to occupy (Hinton, Brzeski, et al., 2017).

Red wolf and coyote packs can occupy areas over long periods, and acquiring a priori information about the space use behaviors of canids can facilitate efficient capture of specific individuals such as breeding females or pups. When targeting specific individuals to capture, Recovery Program biologists relied on land cover characteristics associated with both canid presence and past trapping success to increase the specificity of trapping efforts. Indeed, the RWAMP used placeholders

to eliminate "zones of ignorance," areas where the status of canids was unknown, by which annual trapping and radio-monitoring of placeholders were used to eliminate these zones (Kelly, 2000, Rabon et al., 2013). Consequently, the large-scale, long-term monitoring of canids across the NC Recovery Area allowed the Recovery Program to routinely operate with a priori information and target core areas of canid territories and their preferred land cover types to capture and radio-mark red wolf pups, unknown mates, or to replace malfunctioning radio collars on individuals (Hinton, Brzeski, et al., 2017 and Hinton, White, et al., 2017).

As coyote numbers in the NC Recovery Area increased, the use of sterile coyotes became practical for other purposes. For example, transient coyotes were commonly captured, sterilized, and released by the Recovery Program because it was understood that transients could eventually become placeholders (Hinton, van Manen, & Chamberlain, 2015; Hinton, White, et al., 2017). Additionally, fox-hunting pens, also known as controlled hunting preserves for red foxes (*Vulpes vulpes*) and coyotes, were legal throughout North Carolina, with several operations occurring in the NC Recovery Area (North Carolina Wildlife Resource Commission [NCWRC], 2018). Recovery Program biologists expressed concern that the trafficking of coyotes associated with fox-hunting pens could increase the presence of coyotes in the NC Recovery Area (Hinton et al., 2013; USFWS, 2007). Consequently, the Recovery Program commonly purchased red wolves, coyotes, and hybrids from local trappers at market prices, allowing biologists to develop collaborative relationships within local communities and improve management of red wolves and coyotes. Therefore, the Recovery Program used placeholders flexibly to advance recovery goals while minimizing genetic introgression into the red wolf population.

Our objective was to evaluate the USFWS's management of coyotes in the NC Recovery Area under the context of red wolf recovery in which sterilization was a unique tool used by the Recovery Program to manage coyotes and hybrids. To accomplish this, we identified core components of the Recovery Program's management of coyotes under the RWAMP and provide a suite of analyses to measure the consequences of those actions on the region's red wolf, coyote, and hybrid populations. Using the long-term capture–mark–recapture (CMR) and radio-telemetry data collected by the Recovery Program, we draw heavily on three areas of research: (1) spatial modeling to correlate land cover characteristics with the Recovery Program's relative probability of capture of red wolves, coyotes, and hybrids; (2) survival analysis of radio-marked canids; and (3) population modeling to estimate annual population sizes for the three *Canis*

taxa inhabiting the NC Recovery Area. It is important to note that we analyzed the Recovery Program's long-term monitoring data under an exploratory framework instead of hypothetico-deductive one because sterilization occurred throughout the NC Recovery Area without a control population necessary for measuring the true effect of sterilization (e.g., sterile vs. fertile placeholders). Nevertheless, we believe our assessment of this long-term monitoring data is an important initial step for developing appropriate hypothetico-deductive methods to assess the effect of sterilization on coyote abundance and survival.

STUDY AREA

The 6000-km^2 NC Recovery Area was located on the Albemarle Peninsula of northeastern North Carolina (Beaufort, Dare, Tyrrell, and Washington counties; Figure 1). The region was an intensively farmed agricultural-hardwood bottomland forest system that consisted of predominantly five cover types including coastal bottomland forest (15%), wetland (20%), cropland (30%), commercial pine plantation (15%), and open water (10%). Most pine plantations were owned and operated by Weyerhaeuser Company. Climate was characterized by four distinct seasons similar in duration. Average yearly precipitation was between 122 and 132 cm. Summers were humid, with temperatures ranging between 27 and 38°C. Winter temperatures varied from −4 to 7°C and snow fall occurred occasionally. Further details of the study area are described in Hinton, White, et al. (2017).

MATERIALS AND METHODS

Animal captures and monitoring

Since 1988, the Recovery Program annually trapped red wolves, coyotes, and hybrids during fall and winter and regularly monitored radio-collared animals until they died, or their radio collars failed. During spring, the Recovery Program located dens and daybeds of radio-collared red wolves to count pups and implant passive integrated transponder (PIT) tags in each pup subcutaneously to identify non-collared wolves captured during annual trapping (Beck et al., 2009; Rabon et al., 2013). Further details of the Recovery Program's trapping and monitoring efforts are described in Hinton, Brzeski, et al. (2017); Hinton, White, et al. (2017). To augment annual trapping efforts, the Recovery Program also coordinated with local trappers in the Recovery Area to purchase red wolves, coyotes, and hybrids at market prices to prevent trappers from
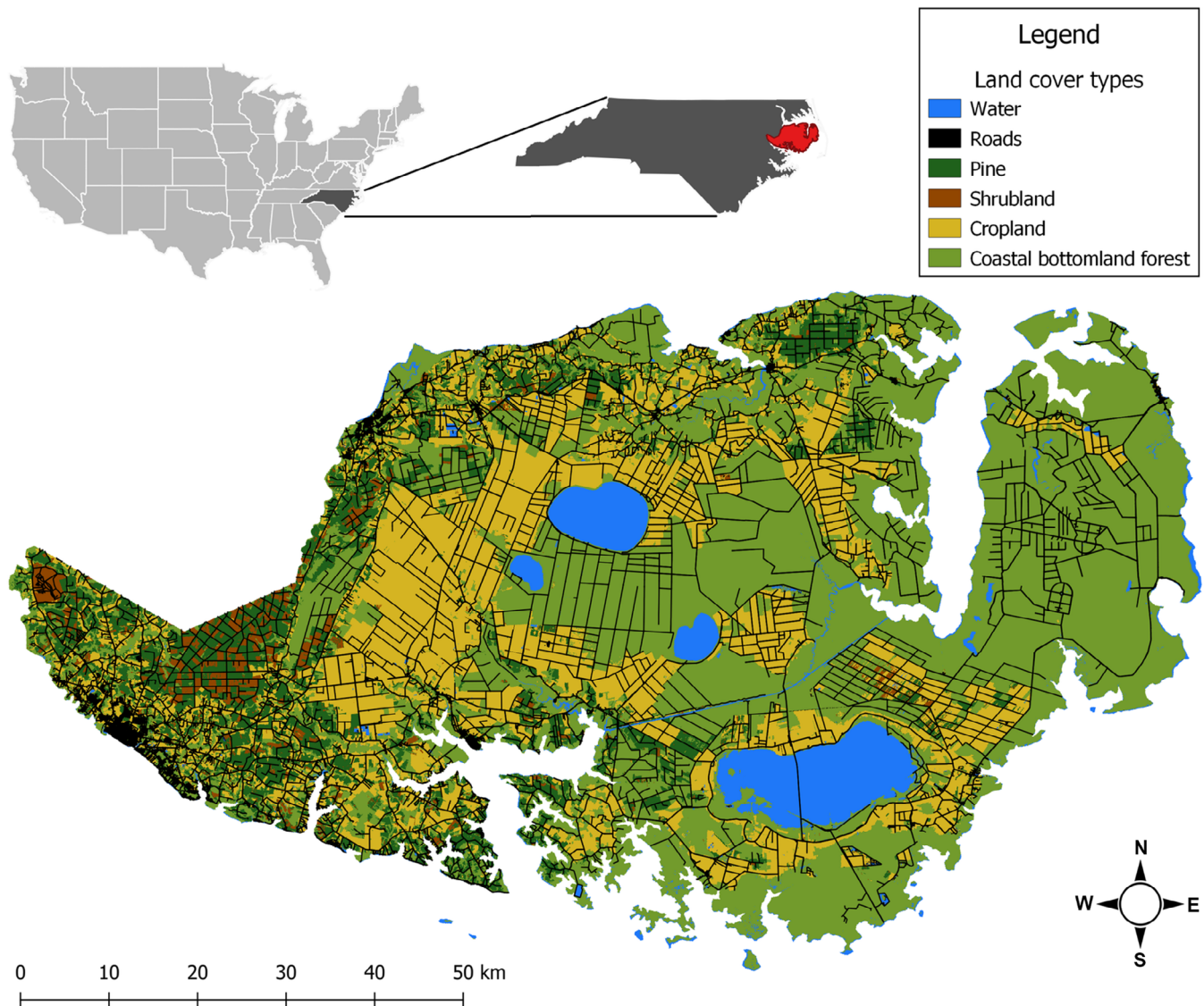
FIGURE 1 Location of the 6000-km^2 Red Wolf Experimental Population Area on the Albemarle Peninsula of northeastern North Carolina.

unknowingly selling wolves and potential placeholders to fox pen operations (USFWS, 2007). The Recovery Program purchased canids from private trappers at $125/individual as market prices for coyotes ranged between $100 and 150/coyote throughout North Carolina (USFWS, unpublished data).

Detailed life-history data on red wolves permitted accurate assignment of ages to wolves (Hinton & Chamberlain, 2014; Hinton, White, et al., 2017), but ages of coyotes and hybrids were estimated using tooth wear and body condition (Gier, 1957; Gipson et al., 2000). All canids were sexed, measured, and weighed, and blood samples were taken for genetic confirmation of taxa. Juvenile (1–2 years old) and adult (≥2 years old) canids were fitted with mortality-sensitive very high frequency (VHF) (Telonics, Mesa, AZ, USA) or global positioning system (Lotek, Ontario, Canada) radio collars. VHF abdominal transmitters (Advanced Telemetry Systems, Insanti, MN, USA) were surgically implanted in red wolf pups <8 months old, if they were below the minimum physical size to wear radio collars. All radio-marked individuals were monitored 2–3 times/week via aerial telemetry.

Prior to their release, coyotes and hybrids were taken to a local veterinary clinic and surgically sterilized with vasectomies and tubal ligations by licensed veterinarians (Gese & Terletzky, 2015). Coyotes and hybrids were euthanized when they were compromised (e.g., diseased or permanently injured), considered as nuisance animals by landowners, or captured in areas already saturated with red wolf and placeholder territories. Therefore, no reproductively intact coyotes or hybrids were monitored by the Recovery Program during our study period.

Animals scheduled for sterilization were held for 1–10 days and typically released within 24–72 h following surgery (Hinton & Chamberlain, 2014). Research techniques and animal care procedures were conducted under permits and standard operating protocols approved by the USFWS and the NCWRC and met the guidelines recommended by the American Society of Mammalogists (Sikes et al., 2011) and best management practices recommended for trapping furbearers in the United States (White et al., 2021).

Our analyses relied on data collected by the Recovery Program on red wolves, coyotes, and hybrids from 1987 to 2014 and reported in Hinton, Brzeski, et al. (2017). However, Hinton, Brzeski, et al. (2017) did not include coyotes and hybrids that the Recovery Program purchased from private trappers in their analysis. For the analyses herein, we relied on both trapline captures (USFWS captures) and purchases (private trapper captures) made by the Recovery Program during 1987–2014. However, because sterilization became a management tool after the implementation of the RWAMP during 2000 (Kelly, 2000) and its use was halted by the USFWS during 2014 (USFWS, 2018), we focused on the years from 2000 to 2013 in our analyses. Data included number of red wolves, coyotes, and hybrids captured, capture location, type of trapper (USFWS vs. private trapper), number of sterile animals released, monitoring duration of radio-marked canids, and causes of death. During processing, coyotes and hybrids were either euthanized or sterilized. Following the release of sterile animals, the duration of monitoring was calculated from the first day of release until the last contact event between monitored animals and the Recovery Program. Last contact events were carcass retrieval in the field, recapture of animals removed from the field, or when the Recovery Program considered animals lost because of collar failure or dispersal from the NC Recovery Area.

Environmental correlates of animal captures

Habitat selection by red wolves, coyotes, and hybrids undoubtedly influenced where animals could be trapped in the NC Recovery Area (Dellinger et al., 2013; Hinton et al., 2016; Hinton, van Manen, & Chamberlain, 2015; Karlin et al., 2016). Therefore, under a framework similar to those used to identify environmental correlates of animal resource use (Northrup et al., 2022), we used generalized linear mixed models (GLMMs) to identify environmental correlates of animal captures in the NC Recovery Area. We followed a second-order resource selection design (Manly et al., 2002) to assess the relationship between land cover characteristics and animal captures.

To accomplish this, we first identified statistically significant areas trapped for red wolves, coyotes, and hybrids by using fixed kernel density estimators (KDEs; Worton, 1989) with the h-plugin smoothing parameter in the "ks" package for program R (Duong, 2007; R Core Development Team, 2020) to generate 99% isopleths. In the same manner that KDEs are commonly used to estimate animal home ranges (Fieberg, 2007; Worton, 1989) and, in studies of road ecology, to identify areas where animals frequently crossed roads (Mohammadi & Kaboli, 2016; Skórka et al., 2015; Yu et al., 2014), we used them to identify statistically bounded areas where Recovery Program biologists and private trappers had a reasonable probability of trapping. Within the estimated areas trapped, we generated random locations (10 times greater than animal-capture locations) to sample land cover availability. We then overlaid animal-capture locations and random locations onto 30-m resolution digital maps of spatial predictors to extract values of land cover types that we suspected influenced the relative probability of capture of red wolves, coyotes, and hybrids.

Within the NC Recovery Area, we developed 14 land cover classes from several national databases. We used the 2011 National Land Cover Database (NLCD; Homer et al., 2015) to develop 10 distance-based land cover classes—distances to cropland (classes 81–82), deciduous forest (class 41), residential/commercial (classes 23–24), grassland (class 71), mixed forest (class 43), pine forest (class 42), pocosin (class 95), shrub/scrub (class 52), water (class 11), and coastal bottomland forest (class 90). We acquired a 2012 road layer from the North Carolina Department of Transportation (2020) to create a distance to roads land cover class. We created distance raster maps for these 11 spatial predictors using the Euclidean distance tool in ArcGIS 10.6 (Environmental Systems Research Institute Inc., Redlands, CA, USA) to calculate the distance from every 30-m pixel to the closest landscape feature. We acquired mean percent canopy cover using the United States Geological Survey (USGS), 2011 NLCD tree-canopy layer (Homer et al., 2015), whereas we determined elevation from a 30-m raster digital elevation model (USGS, 2021). We quantified vegetation biomass using the United States Forest Service (USFS) National Forest Inventory and Analysis dataset (USFS, 2021).

We used principal component analysis (PCA) to reduce dimensionality of our data and extract the dominant, underlying gradients of variation (principal components [PCs]). We used the latent root criterion (PC with eigenvalues ≥1) as a stopping rule to determine the number of significant PCs to retain and interpret (McGarigal et al., 2000). We then based our

interpretation of each PC on those variables with loadings ≥0.50 or ≤−0.50 and placed most emphasis on loadings ≥0.60 or ≤−0.60 (McGarigal et al., 2000). We used the variables with the strongest loadings to interpret the ecological meaning of each PC. The PCs were then used as indicators of land cover complexes and variables of land cover gradients existing in the NC Recovery Area, in which animal captures either increased or decreased with the value of the latent environmental variables.

To model animal captures with land cover correlates, we used a GLMM with a logit link in Program R to evaluate the influence of land cover on the probability of red wolf, coyote, and hybrid captures. We included a random intercept for animal ID for unbalanced animal-capture data, given the clustered nature of the data, in each model using the lme4 package in R (Bates et al., 2014). We modeled animal captures with a binary (0 = random, 1 = capture) response variable. To ensure efficiently derived accurate estimates of land cover availability, we compared characteristics of capture locations to 10 times the number of random locations within the 99% KDE (Northrup et al., 2022). To model the influence of land cover correlates on the relative probability of capture of *Canis* taxa, we constructed separate but identical GLMMs for each taxon and compared the coefficients and their 95% confidence intervals (CIs) (Northrup et al., 2022). As noted by Northrup et al. (2022), nonspatial factors cannot be modeled as covariates in spatial models because these models are typically approximating a Poisson point process model.

We restricted models to first-order terms and explored all possible combinations of our predictors as candidate models to investigate animal-capture probability (Arnold, 2010; Doherty et al., 2012). We evaluated model sets using Akaike information criterion (AIC) and used ΔAIC to select which models best supported factors influencing the capture probabilities of red wolves and placeholders (Burnham & Anderson, 2002). We considered the model with the lowest AIC and the greatest model weight as the best approximating model. However, when model sets had ≥2 models that were within 2 ΔAIC of the top model, we performed model-averaging across the top model set to calculate effect sizes of explanatory variables. Although we acknowledge existing criticism of model-averaging (e.g., Cade, 2015), we believe our PCA eliminated potential dependencies among our land cover variables that could bias parameter interpretations when averaging model parameter estimates.

Causes of death

For red wolves and placeholders, we grouped overall causes of mortality into five categories: management,

anthropogenic, natural, roadkill, and unknown. However, red wolves and coyotes experience different mortality agents within each category. For management, placeholder mortalities caused by management-related activities included deaths resulting from the removal of animals by the Recovery Program to create space for red wolves. Red wolf mortalities caused by management-related activities included deaths related to capture and handling of wolves. Harvest mortalities caused by the public via hunting and trapping were considered anthropogenic mortality for placeholders. Harvest was not a source of mortality for red wolves because killing wolves was illegal; therefore, hunting wolves via shooting, trapping, poisoning, and other forms of foul play by the public were considered illegal. Roadkill was categorized separately from other anthropogenic causes because most incidents of roadkill were likely accidental and without the intent to kill an animal. Natural mortalities were caused by red wolves killing conspecifics (intraspecific strife), wolves killing placeholders (interspecific strife), or disease. We assigned mortalities to the category unknown when there was insufficient evidence to determine the cause of death. We reported observed values for sources of mortality.

Annual apparent survival and abundance estimation

We used multi-year CMR and radio-telemetry data to estimate apparent survival (φ) and annual abundance of red wolves, coyotes, and hybrids each year using the superpopulation parameterization (POPAN; Schwarz & Arnason, 1996) of the Jolly–Seber model (Jolly, 1965; Seber, 1965) in the R package "RMark" (Laake, 2013), which has an integrated interface to the program MARK (White & Burnham, 1999). Since multiple sources of data can be combined in CMR analyses (Lukacs & Burnham, 2005), we combined encounter histories for individuals from capture and radio-telemetry data to calculate more robust estimates of survival and abundance than either data set would provide alone. Coyotes and hybrids that were not released as placeholders and consequently euthanized by the Recovery Program following their capture were censored from our analysis. Therefore, we only used red wolves and placeholders in an open-population POPAN model to acquire abundance estimates of *Canis* taxa in the NC Recovery Area, and we used an open-population model because the study populations were not closed to immigration or emigration between and within years. For example, the Recovery Program periodically released captive-born red wolves into the wild to augment the

reintroduced population (Hinton, White, et al., 2017), and Hinton et al. (2012) reported radio-collared coyotes emigrating out of the NC Recovery Area. All POPAN modeling efforts included identical a priori sets of models that included all possible models with either time-varying (t) or constant ($\cdot$) values of apparent survival, capture probability (p), probability of entry (p_{ent}), and superpopulation size (N). In this context, we defined superpopulation as the total number of animals in the red wolf, coyote, and hybrid populations over the course of the study period.

We used the quasi-likelihood adjustment to AIC (QAIC) to evaluate support among competing models because our capture history data displayed more variation (binomial strings of 0 and 1) than expected by the multinomial statistical model (Anderson et al., 1994; Burnham & Anderson, 2002). When data are over-dispersed, QAIC overcomes shortcomings of the AIC as a metric for model parsimony. We measured overdispersion using the function "release.gof()" in RMark, which accessed the RELEASE goodness-of-fit program implemented through the program MARK, to calculate the value of $\hat{c}$ via TEST2 and TEST3 of Burnham et al. (1987).

RESULTS

Captures and monitoring

From 1987 to 2013, 889 red wolves (425 female; 452 male; 12 unknown), 443 coyotes (224 female; 217 male; 2 unknown), and 296 hybrids (126 female; 156 male; 14 unknown) were captured by the Recovery Program or purchased from private trappers. Approximately 80.2% of the Recovery Program's first encounters with red wolves occurred during spring den checks when pups were located at dens and PIT-tagged, whereas annual trapping during fall and winter accounted for 6.0% of first encounters when wolves were captured and radio-collared. The remaining 13.8% of first encounters with red wolves involved release of captive-born introductions into the wild population via pup fostering (4.2%) or release of juvenile and adult animals (9.6%). Although all encounters with coyotes occurred during annual trapping, the Recovery Program first encountered 87.0% hybrids as trapped animals. The remaining 13.0% of first encounters with hybrids occurred during spring den checks that involved locating dens of red wolves paired with fertile coyotes or hybrids.

Of the 713 PIT-tagged red wolf pups, 69.6% (496 wolves) were later recaptured and radio-collared. Of those recaptures, the Recovery Program purchased 14.1%

from private trappers. Approximately 28.2% (125) of coyotes and 11.8% (35) of hybrids encountered by the Recovery Program were purchased from private trappers. Following the implementation of the RWAMP in 2000 through 2013, the Recovery Program sterilized and released 48.3% (320 individuals) of captured coyotes and hybrids. The proportion of captured coyotes used as placeholders was greater than the proportion of captured hybrids used, in which 69.1% (221 individuals) of all placeholders were coyotes.

Under the RWAMP (2000–2013), radio-collared red wolves were monitored for an average of 1166.0 days (SD = 1011.9) and ranged between 5 and 4336 days. Following their release, placeholders were monitored for an average of 713.5 days (SD = 762.7) and ranged between 1 and 4179 days. Approximately 53.7% of red wolves and 33.0% of placeholders were monitored for ≥ 2 years. The Recovery Program lost contact with 72 radio-collared red wolves and 75 placeholders.

Environmental correlates of animal captures

During 2000–2013, the Recovery Program captured 1252 animals (756 red wolves, 309 coyotes, 187 hybrids) across the 6000-km^2 peninsula at a rate of 1 capture/3.8 days. The Recovery Program accounted for 91.1% of animal captures, and 44.3% of all animal captures were recaptures. The estimated 99% isopleth for animal captures encompassed 3746.6 km^2 (62.4%) of the NC Recovery Area.

The first four PCs (PC1, PC2, PC3, and PC4) explained 38.5%, 15.3%, 12.9%, and 7.1% of the cumulative variation in our land cover predictors, respectively, and were the only PC scores with eigenvalues ≥ 1. Since the first four axes explained 73.8% of the total variance, we deemed the four-dimensional solution adequate. PC1 consisted of strong positive loadings for distances from shrub/scrub, pine forest, mixed forest, grassland, residential/commercial, deciduous forest, and croplands—these variables contributed 93.7% of PC1's quality of representation (Figure 2). In conjunction with the surface map of PC1 (Figure 3), we interpreted PC1 as a negative relationship (decreasing PC scores) with the NC Recovery Area's fragmented land cover on private lands and a positive relationship (increasing PC scores) with the more contiguous cover, such as pocosin, coastal bottomland forest, and lakes, on federal lands. PC2 consisted of large positive loadings for distances from coastal bottomland forest and pocosin and large negative loadings for biomass and canopy cover—contributing 85.8% of PC2's quality of representation (Figure 2). The strong negative loadings for
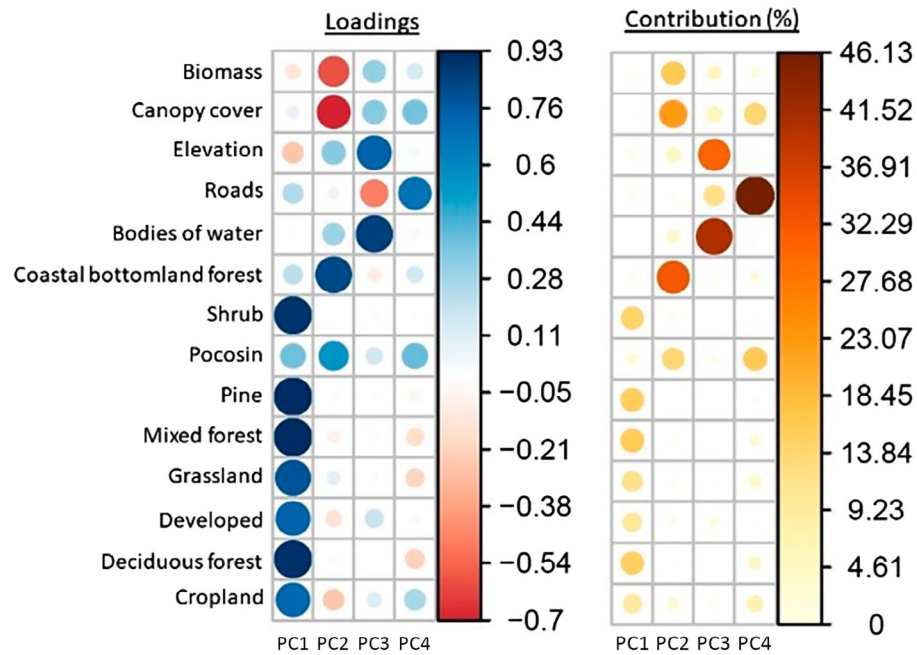
FIGURE 2 Loadings and contributions of the four primary principal components from our principal component analysis. Environmental variables are represented on each row.
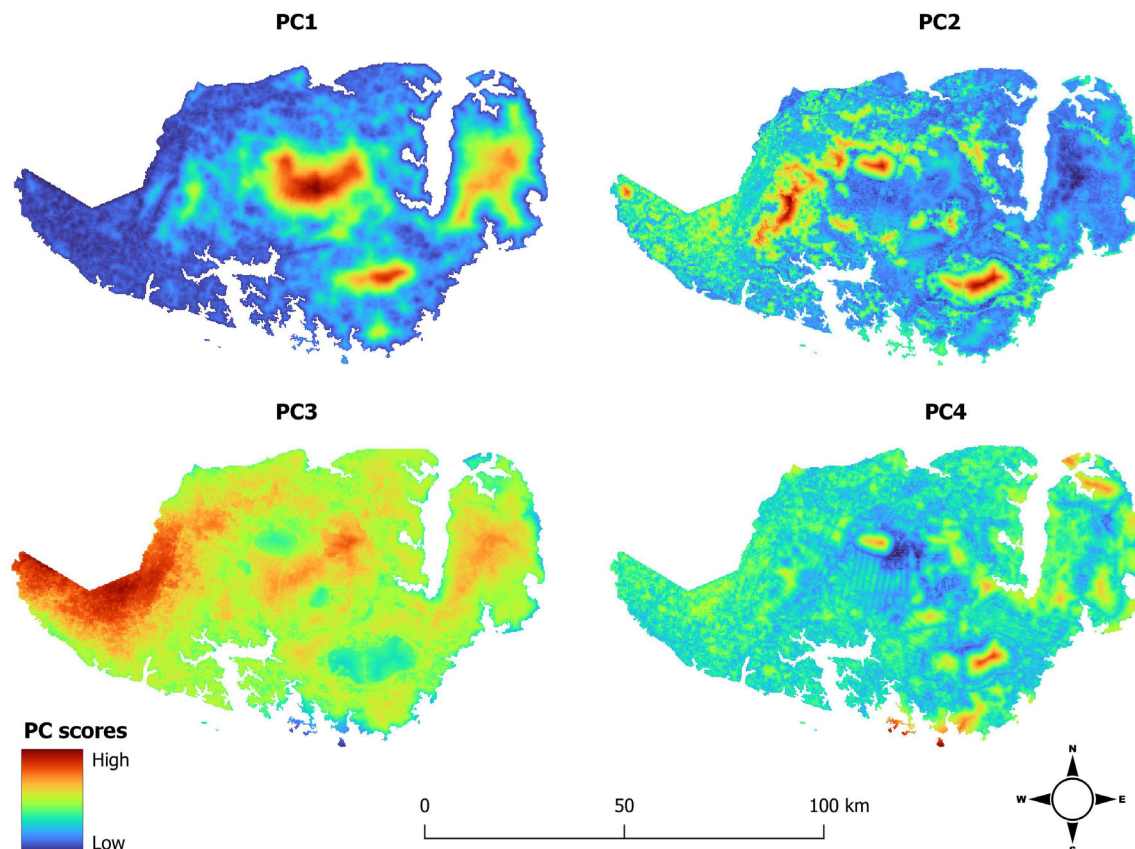

FIGURE 3 Surface maps of each of the four primary principal component (PC) scores across the 6000-km^2 North Carolina Red Wolf Recovery Area. Contiguous land cover, low vegetation density, elevation, and distance from roads are represented by PC1, PC2, PC3, and PC4, respectively.

biomass and canopy cover as well as the surface map of PC2 scores (Figure 3) lead us to interpret increasing PC2 scores as representing areas of low vegetation density such as croplands and lakes. PC3 consisted of strong positive loadings for elevation and distance from large bodies of water—contributing 71.1% of PC3's quality of representation (Figure 2). Consequently, we interpreted increasing PC3 scores as representing areas of increasing elevation and distance from bodies of water (Figure 3). Finally, PC4 consisted of strong loading for distances from roads and pocosin—contributing 62.3% of PC4's

quality of representation (Figure 2). Both loadings and the surface map of PC4 scores (Figure 3) lead us to interpret increasing PC4 scores as representative of areas away from roads.

For red wolf captures, the global model was the top model in which the relative probability of capture of wolves was greatest in dry areas proximate to roads and characterized by low canopy cover and vegetation density, such as cropland (Tables 1 and 2, Figure 4). Similarly, the global model was the top model in which the relative probability of capture of coyotes was greatest

TABLE 1 Summary of the top generalized linear models (cumulative Akaike weight ≤0.99) for explaining correlations of land cover types with the relative probability of capture of red wolves, coyotes, and hybrids in eastern North Carolina, USA, 2000–2013.

Taxon	Model	k	AIC_c	ΔAIC_c	ω_i	Cumulative ω
Red wolf	PC1 + PC2 + PC3 + PC4	6	4817.07	0.00	1.00	1.00
	PC1 + PC3 + PC4	5	4838.58	21.51	0.00	1.00
Coyote	PC1 + PC2 + PC3 + PC4	6	2048.11	0.00	1.00	1.00
	PC1 + PC3	3	2059.62	11.51	0.00	0.00
Hybrid	PC1 + PC2 + PC3 + PC4	6	1232.82	0.00	0.37	0.37
	PC1 + PC2 + PC4	5	1232.87	0.05	0.36	0.73
	PC1 + PC4	4	1234.76	1.93	0.14	0.87
	PC1 + PC3 + PC4	5	1234.79	1.96	0.13	1.00
	PC2 + PC4	4	1247.55	14.72	0.00	1.00

Note: PC1, contiguous land cover; PC2, low vegetation density; PC3, elevation; and PC4, distance from roads. Shown are Akaike information criterion for small sample sizes (AIC_c), differences among AIC_c (ΔAIC), AIC_c weights (ω_i), and cumulative AIC_c weights.

TABLE 2 Parameter estimates of the global generalized linear models for explaining correlations of land cover types with the relative probability of capture of red wolves, coyotes, and hybrids in eastern North Carolina, USA, 2000–2013.

Taxon	Model variables	β	SE	95% CI
Red wolf	Intercept	−2.754	0.055	−2.862, −2.647
	PC1	−0.123	0.022	−0.166, −0.080
	PC2	0.138	0.028	0.084, 0.194
	PC3	0.296	0.050	0.198, 0.395
	PC4	−0.912	0.060	−1.029, −0.795
Coyote	Intercept	−2.711	0.084	−2.877, −2.545
	PC1	−0.248	0.039	−0.323, −0.172
	PC2	0.182	0.043	0.098, 0.265
	PC3	0.285	0.077	0.134, 0.436
	PC4	−0.844	0.097	−1.033, −0.655
Hybrid	Intercept	−2.583	0.101	−2.782, −2.385
	PC1	−0.191	0.048	−0.284, −0.098
	PC2	0.113	0.055	0.004, 0.221
	PC3	0.140	0.097	−0.050, 0.331
	PC4	−0.643	0.118	−0.873, −0.413

Note: PC1, contiguous land cover; PC2, low vegetation density; PC3, elevation; and PC4, distance from roads. Shown are regression coefficients (β), standard error (SE), and 95% confidence intervals (CI).
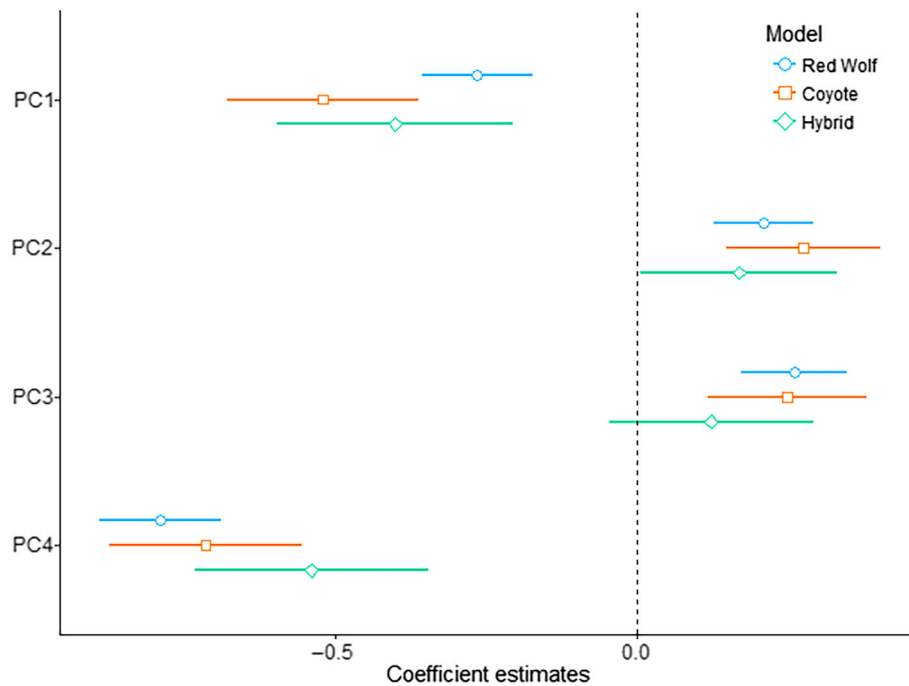
FIGURE 4 Parameter estimates from generalized linear mixed models for red wolves, coyotes, and hybrids captured in the Red Wolf Recovery Area of northeastern North Carolina from 1988 to 2013. The midpoint location and 95% CIs of each distribution are represented by shapes and lines, respectively. Contiguous land cover, low vegetation density, elevation, and distance from roads are represented by PC1, PC2, PC3, and PC4, respectively.

in areas proximate to roads and characterized as dry with low canopy cover and vegetation density (Tables 1 and 2, Figure 4). Although the global model was the top model indicating that all spatial predictors were informative (Table 1), the three next best models had ΔAIC$_c$ of <2. Following Burnham and Anderson (2002), we averaged the coefficient estimates of the top four models (Table 2). Hybrids, like red wolves and coyotes, were captured in predominantly dry areas with low canopy cover and vegetation density proximate to roads (Table 2, Figure 4).

Causes of death

Under the RWAMP (2000–2013), the Recovery Program documented 273 known fates for red wolves in which 65.6% of deaths were attributed to anthropogenic causes such as shooting deaths (30.4%), roadkill (17.2%), management (7.7%), and other human causes (10.3%). Natural causes such as health (10.3%) and intraspecific strife (5.1%) accounted for 15.4% of red wolf deaths, whereas unknown causes accounted for 19.0% of deaths.

Of the 535 known fates documented for coyotes and hybrids, anthropogenic sources of mortality accounted for 91.2% of deaths, with management actions by the Recovery Program contributing to 76.6% of all known coyote and hybrid deaths. Once sterilized and released, the Recovery Program documented 194 known fates for

placeholders. Approximately 74.2% of placeholder deaths were attributed to anthropogenic causes such as management (41.2%), harvest (i.e., shooting and trapping; 22.2%), and roadkill (10.8%), whereas unknown causes accounted for 15.5% of deaths. Interspecific strife was the only known natural cause of death for placeholders and accounted for 10.3% of deaths.

Annual apparent survival and abundance

For our POPAN analysis, $\varphi(\cdot)p(\cdot)p_{ent}(t)N(\cdot)$ was the most supported model in the candidate model sets for red wolves, coyotes, and hybrids, indicating constant apparent survival and capture probability and time-dependent recruitment for all three taxa (Table 3).

Apparent annual survival and recapture probabilities for red wolves were estimated at 0.670 (SE = 0.009, 95% CI = 0.652–0.688) and 0.978 (SE = 0.004, 95% CI = 0.968–0.985), respectively. The probability of entry for red wolves during 2000–2013 ranged from 0.037 to 0.064 (Figure 5). The red wolf superpopulation was 951, in which 93.5% (889 wolves) of the population was known to the Recovery Program. Annual population abundance for red wolves ranged between 102 and 151 red wolves between 2000 and 2013, with peak abundance during 2006 (Figure 6). Red wolf density ranged between 17 and 25 red wolves/1000 km^2.

TABLE 3 Summary of the top five POPAN model set for red wolves, coyotes, and hybrids based on the corrected quasi-Akaike information criterion (QAIC) with adjusted $\hat{c}$.

Taxon	Model	k	QDeviance	ΔQAIC	Qω_i	$\hat{c}$
Red wolf	$\Phi(\cdot)p(\cdot)b(t)N(\cdot)$	34	−1192.20	0.00	1.00	4.38
	$\Phi(\cdot)p(\cdot)b(\cdot)N(\cdot)$	4	−1113.15	18.19	0.00	4.38
	$\Phi(t)p(\cdot)b(t)N(\cdot)$	64	−1204.95	49.46	0.00	4.38
	$\Phi(\cdot)p(t)b(t)N(\cdot)$	65	−1199.51	57.00	0.00	4.38
	$\Phi(t)p(\cdot)b(\cdot)N(\cdot)$	34	−1125.88	66.32	0.00	4.38
Coyote	$\Phi(\cdot)p(\cdot)b(t)N(\cdot)$	29	−861.76	0.00	1.00	2.28
	$\Phi(t)p(\cdot)b(t)N(\cdot)$	54	−905.54	12.56	0.00	2.28
	$\Phi(\cdot)p(t)b(t)N(\cdot)$	55	−871.20	49.24	0.00	2.28
	$\Phi(t)p(t)b(t)N(\cdot)$	80	−904.92	76.41	0.00	2.28
	$\Phi(\cdot)p(t)b(\cdot)N(\cdot)$	30	−706.00	157.94	0.00	2.28
Hybrid	$\Phi(\cdot)p(\cdot)b(t)N(\cdot)$	28	−1106.44	0.00	1.00	1.28
	$\Phi(t)p(\cdot)b(t)N(\cdot)$	52	−1153.69	14.16	0.00	1.28
	$\Phi(t)p(t)b(t)N(\cdot)$	53	−1106.44	64.18	0.00	1.28
	$\Phi(t)p(t)b(t)N(\cdot)$	77	−1153.67	89.56	0.00	1.28
	$\Phi(\cdot)p(\cdot)b(\cdot)N(\cdot)$	4	−956.09	97.44	0.00	1.28

Note: Model names indicate if survival (Φ), probability of capture (p), probability of entry (b), and superpopulation size (N) were held constant ($\cdot$) or varied with time (t). ΔQAIC is the difference in QAIC value between a model and the most parsimonious model. Model weight indicates the support for a model. The number of parameters specifies the number of variables estimated for a model. QDeviance is the deviance of a model from the fully saturated model.
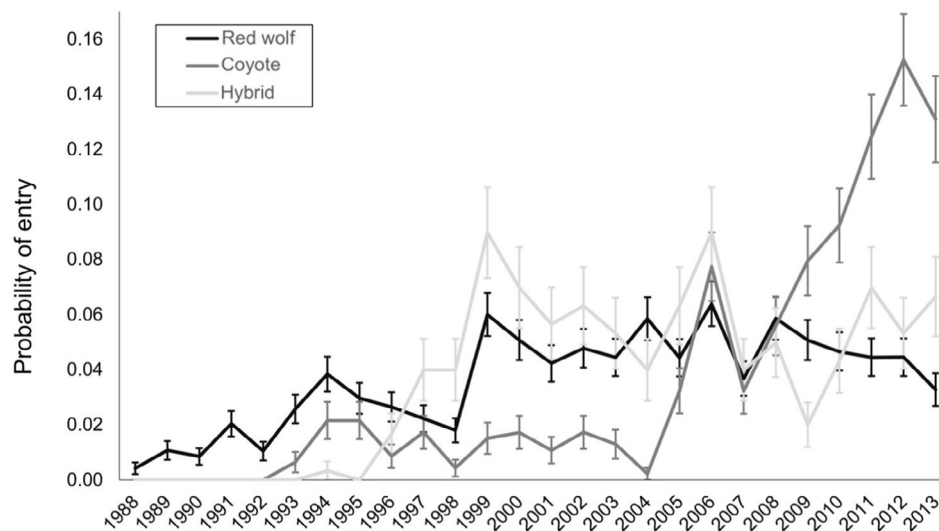

FIGURE 5 Probability of new red wolves, coyotes, and hybrids entering the Red Wolf Recovery Area of northeastern North Carolina from 1988 to 2013. Parameter estimates for the probability of entry (b) were calculated by program MARK using POPAN models. Vertical bars indicate standard errors.

For coyotes, apparent annual survival and recapture probabilities were estimated at 0.543 (SE = 0.019, 95% CI = 0.507–0.580) and 0.998 (SE = 0.002, 95% CI = 0.984–0.999), respectively. The probability of entry for coyotes during 2000–2013 ranged from 0.002 to 0.154 (Figure 5). The coyote superpopulation was 466 in which 47.4% (221 coyotes) of the population was known to the Recovery Program. Annual population abundance of coyotes ranged between 15 and 129 coyotes between 2000 and 2013, with peak abundance during 2013 (Figure 6). Coyote density ranged between 2.5 and 21.5 coyotes/1000 km^2.

Apparent annual survival and recapture probabilities for hybrids were estimated at 0.712 (SE = 0.024,
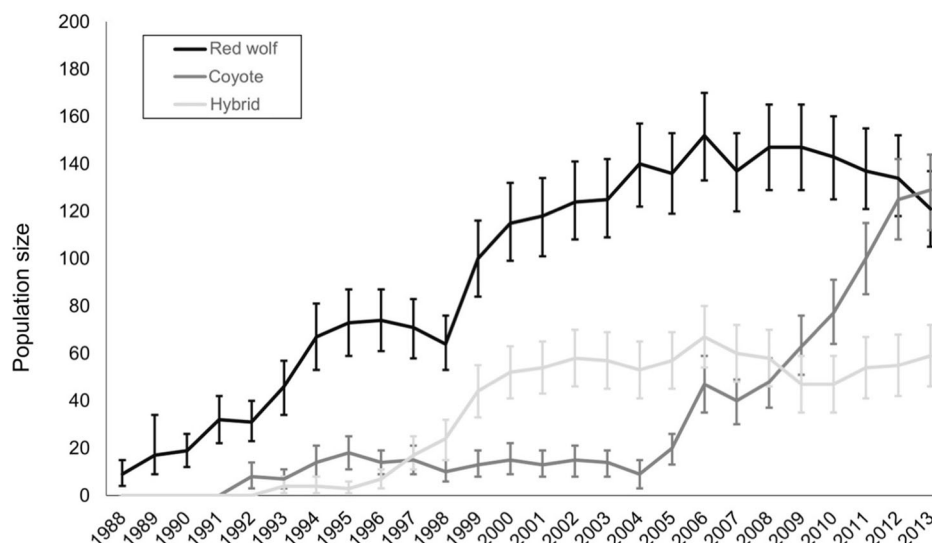
FIGURE 6 Population size of red wolves, coyotes, and hybrids in the Red Wolf Recovery Area of northeastern North Carolina from 1988 to 2013. Population estimates were calculated by the program MARK using POPAN models. Vertical bars indicate 95% CIs.

95% CI = 0.662–0.756) and 1.00 (SE = 0.000, 95% CI = 1.000–1.000), respectively. The probability of entrance for hybrids during 2000–2013 ranged from 0.010 to 0.090 (Figure 5). The hybrid superpopulation was 301, in which 32.9% (99 hybrids) of the population was known to the Recovery Program. Annual population abundance ranged between 44 and 67 hybrids between 2000 and 2013, with peak abundance during 2006 (Figure 6). Hybrid density ranged between 7.3 and 11.2 hybrids/1000 km^2.

DISCUSSION

Although it was believed that coyotes were absent from the Recovery Area in 1987 when red wolves were reintroduced (Hinton et al., 2013; Stoskopf et al., 2005), the Recovery Program's records reported the presence of six male coyotes in the region during May 1987. Additionally, DeBow et al. (1998) reported the presence of coyotes in four of the five counties comprising the NC Recovery Area by 1988. Based on the Recovery Program's trapline data, coyote presence in the Recovery Area was low (5.4 captures/year) from 1987 to 1999 and remained low (6.7 captures/year) from 2000 to 2006 when the Recovery Program implemented the RWAMP and began using placeholders. By 2006, the red wolf population comprised 15 known packs and peaked with 151 wolves. However, after 2006, coyote captures increased considerably (42.9 captures/year) and was correlated with increased shooting deaths and pack disbandment of red wolves (Hinton, Ashley, et al., 2017; Hinton, White, et al., 2017). From 2006 to 2013, the coyote population increased annually, whereas the red wolf population

plateaued before declining after 2013 (Agan et al., 2021), providing further support that population stagnation and decline of wolves caused by anthropogenic mortality in the NC Recovery Area contributed to increasing coyote numbers (Figure 6; Hinton, Brzeski, et al., 2017; Hinton, White, et al., 2017). Unfortunately, it is difficult to measure the direct impact that red wolves and sterilization had on limiting coyotes in the NC Recovery Area because reliable estimates of coyote numbers were lacking for the surrounding areas where red wolves and sterilization were absent. As for hybrids, we estimated an abundance of 47–67 hybrids/year between 2000 and 2013. Additionally, few hybrids were detected outside the NC Recovery Area (Bohling et al., 2016). Both findings indicate that hybrids were rare in northeastern North Carolina because of active management to suppress hybridization (Gese & Terletzky, 2015) and assortative mating by red wolves (Bohling et al., 2016; Hinton et al., 2018). Nevertheless, results from our assessment provide valuable insights into several areas of red wolf recovery and coyote management.

Environmental correlates of animal captures

In the NC Recovery Area, red wolves, coyotes, and hybrids commonly establish territories along cropland–forest edges (Hinton et al., 2016; Hinton, van Manen, & Chamberlain, 2015), and this selection for croplands influenced where Recovery Program biologists established traplines to capture animals. Typically, biologists trapped road networks in croplands proximate to commercial pine plantations and forested

federal lands that were used by red wolves and coyotes as denning areas (Hinton, unpublished data). Given this approach to capturing animals, it was unsurprising that red wolves, coyotes, and hybrids were caught in areas close to roads and with low canopy cover (i.e., cropland), as these cover types were commonly associated with movement and foraging by wolves and coyotes (Dellinger et al., 2013; Hinton et al., 2016; Hinton, Ashley, et al., 2017; Hinton, van Manen, & Chamberlain, 2015; Karlin et al., 2016).

Overall, we believe potential trapping biases in our animal-capture data were minimized by the Recovery Program's large-scale, long-term trapping and monitoring of juvenile and adult red wolves, coyotes, and hybrids and the Program's annual spring den checks to monitor pup production. These management practices likely minimized common biases that occur when subsamples are not representative of the entire population. For example, under the RWAMP during 2000–2013, the Recovery Program's trapping efforts accounted for 91.1% of all captures and covered 62.4% of the 6000-km^2 NC Recovery Area. Additionally, 44.3% of the 1252 animal captures were previously trapped and radio-marked canids (trap-educated animals). Given the high recapture rates of red wolves and placeholders on traplines, our results do not support conclusions of spatial bias in coyote captures by which individuals were least vulnerable to capture within frequently used areas of their territories (Gipson & Kamler, 2003; Windberg & Knowlton, 1990). Instead, animal captures were influenced by the Recovery Program's a priori information that allowed biologists to increase their probability of capturing individuals from specific areas by targeting core areas of canid territories or land cover known to be favored by red wolves, coyotes, and hybrids.

Monitoring duration and sources of mortality

Approximately 48.3% of coyotes and hybrids encountered by the Recovery Program between 2000 and 2013 were sterilized and released as placeholders, and, on average, placeholders were monitored for nearly 2 years. Coyotes were predominately used as placeholders, as most hybrids were euthanized following capture. Despite the coyote's ability to disperse long distances and leave the NC Recovery Area (Hinton et al., 2012), most placeholders (79.7%) remained in the NC Recovery Area and were monitored until their death by the Recovery Program. Our previous research reported that the Recovery Program annually monitored 20 sterile coyotes/year and 12 coyote pairs/year (Hinton, van Manen, & Chamberlain, 2015) during 2009–2011 and 8 congeneric pairs/year from 2000 to

2013 (Hinton, Brzeski, et al., 2017). As documented by Hinton, van Manen, and Chamberlain (2015), many sterile coyotes were transient at capture, and they suggested that approximately 70% of coyotes in the NC Recovery Area were residents. This estimate is comparable with the number of placeholders that settled into territories and were monitored until their deaths. Undoubtedly, unreported killings contributed to the proportion of placeholders that disappeared but differentiating resident from transient animals required ≥4 months of monitoring unless residency could be confirmed via field observations (Hinton, van Manen, & Chamberlain, 2015). It was not unusual for placeholders, assumed to be resident animals at capture, to abandon areas after exhibiting several weeks of localized, resident-like space use and establish territories elsewhere, or to have been residents who were displaced from their territories but established new ones following a period of transiency (Hinton, van Manen, & Chamberlain, 2015).

Overall, the proportion of placeholder deaths attributed to our five categories of mortality (management actions, harvest, interspecific strife, roadkill, and unknown) ranged between 10.3% and 41.2%, indicating that placeholders died of a plurality of causes. However, most of those causes were anthropogenic (i.e., USFWS management, shooting deaths, and roadkill). From 2000 to 2013, 63.4% of placeholder deaths were attributed to the deliberate take of individuals through management actions (41.2%) and harvest (22.2%). Over time, the proportion of placeholder deaths caused by management actions declined, whereas the proportion of deaths caused by shootings did not increase. As noted by Hinton, White et al. (2017), shooting deaths of red wolves increased after 2006, which caused the Recovery Program to increasingly rely on placeholders to fill vacancies that wolf mortalities created on the landscape. More specifically, Hinton, Brzeski, et al. (2017) reported that shooting deaths of red wolves during the fall and winter hunting season was the primary cause of disbandment for wolf packs and prevented long-term pairings of wolves. During 2006–2013, coyotes increasingly replaced red wolves in areas where packs disbanded following gunshot mortalities, which further reduced the ability of surviving wolves to find conspecific mates and facilitated wolf pairings with coyotes (Hinton, Brzeski, et al., 2017). As the red wolf population stagnated and coyotes increased, fewer opportunities arose for the Recovery Program to remove placeholders to create vacancies for wolves because fewer wolves were present to fill vacancies. Consequently, the proportion of placeholders removed by the Recovery Program became fewer and the duration of monitoring placeholders increased.

Shooting deaths of placeholders attributed to 20.1% of known deaths, whereas 30.6% of red wolf deaths were

caused by shootings. Similarly, fewer placeholder deaths were attributed to roadkill than were red wolf deaths (10.8% vs. 17.3%). These discrepancies are likely attributed to two reasons. First, unlike for red wolves, the Recovery Program was a significant source of mortality for coyotes, and management actions likely reduced the number of coyotes that would have been harvested or struck by drivers in the NC Recovery Area. Second, when compared to red wolves, the smaller body size of coyotes may have reduced their risk and exposure to shooting deaths.

Interspecific strife with red wolves was the only natural source of mortality for placeholders and accounted for 10.3% of known deaths. As with shooting and vehicular deaths, lethal management combined with sterilization may have reduced interspecific strife between red wolves and placeholders. Specifically, lethal management removed fertile coyotes and hybrids from areas and left behind fewer animals as placeholders before red wolves had opportunities to displace or kill coyotes and hybrids. Additionally, sterilization eliminated the presence of coyote and hybrid offspring proximate to red wolf territories, which further reduced the number of interspecific interactions wolves experienced. Regardless, the proportion of placeholders killed by red wolves was like those reported in the Greater Yellowstone Ecosystem where gray wolf–coyote interactions were well studied. For example, Berger and Gese (2007) reported that 16% (5 of 32) of radio-marked coyotes were killed by gray wolves, and Merkle et al. (2009) reported that 7% of 337 documented gray wolf–coyote interactions resulted in the death of a coyote. However, it is important to note that red wolves do not interact with coyotes over ungulate carcasses, as commonly observed with gray wolves and coyotes. As reported by Hinton, Ashley, et al. (2017), scavenging opportunities for coyotes in the NC Recovery Area were scarce because red wolf and coyote territories did not overlap, white-tailed deer were relatively small ungulates that were quickly consumed by wolf packs, and coyotes were capable of killing deer throughout the year. Instead, interspecific strife between red wolves and coyotes occurred over space and mating opportunities and involved wolves usurping placeholders from areas to acquire their space and, at times, mates. If placeholders were not killed by red wolves, then they were displaced from their territories and forced into transiency.

Annual apparent survival and abundance estimates

Annual apparent survival for red wolves and hybrids was greater than survival for coyotes, with wolves and hybrids exhibiting similar annual survival. This is contrary to the findings of Gese and Terletzky (2015) in which they reported mean annual survival rates were lowest for red wolves, intermediate for coyotes, and greatest for hybrids. However, they censored lethal removal of placeholders by the Recovery Program from their survival analysis, whereas our analysis used all mortalities experienced by placeholders. By accounting for lethal removal of placeholders via federal management, we believe our results reflect annual survival rates experienced by red wolves and placeholders under conditions created by the RWAMP, whereas survival rates estimated by Gese and Terletzky (2015) likely reflect natural survival without management. Given that our survival rates were 30% lower (0.543 vs. 0.843) than Gese and Terletzky (2015), we suggest that difference may reflect the impact that the RWAMP had on coyote survival in the NC Recovery Area.

Although coyote occurrence in the NC Recovery Area has increased in recent decades (Gese et al., 2015; Hinton, Brzeski, et al., 2017), previous research did not provide robust estimates of abundance. From 1992 to 2013, coyote density in the Recovery Area ranged from 1.3 to 21.5 coyotes/1000 km^2, with the greatest increases in density occurring during 2007–2013, likely driven by time-varying probability of entry (Figure 5). The net entry results of our POPAN model include net births and immigration (Schwarz & Arnason, 2009). Approximately 71% of the total *Canis* superpopulation was marked by the Recovery Program during spring den checks and annual trapping, and the remaining 29% of the superpopulation predominantly consisted of fertile coyotes and hybrids. Undoubtedly, some of these fertile coyotes and hybrids intermingled with each other and some of the unknown red wolves to form breeding pairs and accounted for local births in the NC Recovery Area. However, given the presence of sterilization, lethal removal, and interspecific competition across most of the NC Recovery Area, we believe coyotes entered the population mostly through immigration from outside areas and, to a lesser extent, through births in suitable areas of the NC Recovery Area where placeholder and red wolf territories were absent. Despite the increase in coyote abundance during 2005–2013, red wolf abundance was estimated to be greater in all years, except for 2012–2013 (Figure 6).

When compared to coyote densities reported in other regions of North America (e.g., see tab. 22.2 in Bekoff & Gese, 2003; abstract summaries in Mastro et al., 2012), those in the NC Recovery Area were lower than densities reported in all regions except those reported at the coyote's northernmost range limits (e.g., O'Donoghue et al., 1997). We also report lower coyote density estimates than those reported in more recent studies such as those conducted in southwest Arizona (53.0–112 coyotes/1000 km^2;

Woodruff et al., 2021), the Great Basin Desert of Utah (70–80 coyotes/1000 km^2; Lonsinger et al., 2018), the Appalachian region of Virginia (24–90 coyotes/1000 km^2; Morin et al., 2016), and the Savannah River region of South Carolina (800–1500 coyotes/1000 km^2; Kilgo et al., 2017). Of those studies, Appalachia and the Savannah River region were neighboring areas of the NC Recovery Area exhibiting greater densities of coyotes. Although our greatest density estimate (21.5 coyotes/1000 km^2) was 40× lower than the lowest density estimate (800 coyotes/1000 km^2) reported by Kilgo et al. (2017), their estimate is likely an extreme outlier. We believe the large difference between our coyote density estimates and those reported by Kilgo et al. (2017) was caused by the lethal removal of 474 coyotes from the Savannah River Site during a 3-year period that facilitated strong compensatory immigration to the area (Kierepka et al., 2017). Furthermore, the removal of 1.6 coyotes/km^2 reported by Kilgo et al. (2017) was for three 32-km^2 treatment units considerably smaller than the NC Recovery Area and would equate to the removal of 9600 coyotes from the 6000-km^2 region. Regardless, we believe coyote densities in the NC Recovery Area during 2000–2013 can be described as low.

We suggest that sterilization and red wolf presence likely reduced coyote abundance by eliminating reproductive space for coyotes, with lethal control further reducing the number of coyotes traversing the NC Recovery Area. For example, it is assumed that inundated habitats such as coastal bottomland forests and marshes reduced suitable habitat for red wolves and coyotes in the NC Recovery Area to about 3600 km^2 (Hinton et al., 2016; Hinton, van Manen, & Chamberlain, 2015; USFWS, 2007). The average coyote home range in the NC Recovery Area was 27.2 km^2 (Hinton, van Manen, & Chamberlain, 2015), and between 2009 and 2011, the Recovery Program monitored 20 placeholder (12 conspecific and 8 congeneric) home ranges/year (Hinton, Brzeski, et al., 2017; Hinton, van Manen, & Chamberlain, 2015). During that period, 16 red wolf home ranges were monitored each year by the Recovery Program and averaged 68.4 km^2 (Hinton et al., 2016; Hinton, Brzeski, et al., 2017). This indicates that placeholders and red wolves prevented coyote reproduction on 544 and 1094 km^2 of the NC Recovery Area, respectively. These areas accounted for 45.5% of suitable space in the Recovery Area during 2009–2011 and experienced a density of 12 coyotes/1000 km^2. Without sterilization and the presence of red wolves, it is plausible those areas could have been occupied by 60 coyote packs and, assuming two breeders and four offspring per pack, inhabited by 360 coyotes (220 coyotes/1000 km^2). Given the limited breeding space for coyotes in the NC Recovery Area, the dynamic nature of coyote survival, territories, and pack sizes, and density dependence, we believe 500–700 coyotes (83–117 coyotes/1000 km^2) could inhabit the 6000-km^2 area in the absence of red wolves and federal management. However, this is a back-of-the-napkin estimate influenced by our experience of studying red wolves and coyotes on the Albemarle Peninsula, and we believe a more sophisticated and appropriate analysis (e.g., model simulations incorporating coyote space use and density dependence) is needed.

CONCLUSIONS

While an effective management strategy to control coyote populations has been elusive, the use of placeholders provided valuable and unique insights into the population ecology of coyotes, their interactions with red wolves, and the potential use of sterilization in the management of coyotes. Gese and Terletzky (2015) emphasized that sterilization was not used to limit the distribution or size of the coyote population, but instead was used to reduce incidents of hybridization between coyotes and red wolves and genetic introgression into the wild wolf population. We do not disagree with this, but we note that the RWAMP called for saturating the NC Recovery Area, with red wolf territories facilitated by using placeholders (Rabon et al., 2013). For example, the most recent RWAMP stated that "sterilization is a method that allows territorial space to be held until that animal can be replaced naturally or by management actions" (Rabon et al., 2013). Indeed, the term placeholder implies the use of sterile animals as an intermediate step to eliminate coyotes and hybrids from areas targeted for red wolf recovery. Although the purpose of sterilization in-and-of itself was to prevent hybridization, the overall goal of the placeholder concept, as noted in the RWAMP and demonstrated by field operations conducted by the Recovery Program, was to transition areas from coyote occupancy to red wolf occupancy. Therefore, we emphasize that sterilization was used by the Recovery Program to facilitate coyote population management, which included minimizing incidents of hybridization, disrupting coyote reproduction, and reducing coyote abundance in areas of the NC Recovery Area. Although the lack of a control population prevented us from conducting hypotheses to determine the cause of low coyote abundance in the NC Recovery Area during 2000–2013, we offer the combination of red wolf presence and coyote sterilization, and to a lesser extent, lethal control, likely suppressed coyote abundance and density in the area. We also suggest that more research is needed before sterilization can be recommended as a viable tool for managing coyote populations.

AUTHOR CONTRIBUTIONS

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

The authors have declared no conflict of interest.

DATA AVAILABILITY STATEMENT

Data that support this study are sensitive and cannot be provided publicly without a memorandum of agreement with the United States Fish and Wildlife Service Red Wolf Recovery Program. Requests can be sent to redwolf@fws.gov.

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