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Research Article

Survival and Population Size Estimates of the Red Wolf

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ABSTRACT Evaluating anthropogenic mortality is important to develop conservation strategies for red wolf (*Canis lupus*) recovery. We used 26 years of population data in a generalized linear mixed model to examine trends in cause-specific mortality and a known-fate model in Program MARK to estimate survival rates for the reintroduced red wolf population in North Carolina, USA. We found the proportion of mortality attributable to anthropogenic causes, specifically mortality caused by gunshot during fall and winter hunting seasons (Oct–Dec), increased significantly since 2000 and became the leading cause of red wolf death. Mortality rates were greatest for red wolves <4 years of age, and we suspect inexperience with human activities (e.g., hunting) likely caused younger wolves to be more susceptible to opportunistic killing by hunters. Since 1987, the red wolf population steadily grew and peaked at an estimated 151 individuals during 2005 but declined to 45–60 by 2016. To reduce the negative effects of anthropogenic mortality and ensure long-term persistence of red wolves, the United States Fish and Wildlife Service (USFWS) will need to re-implement previous long-standing and proven management practices (e.g., Red Wolf Adaptive Management Plan) on public and private lands and cease issuing take permits. The USFWS will also need to establish an effective management response to mitigate gunshot mortality through stronger regulation of coyote (*Canis latrans*) hunting and provide adequate ecologically and biologically supported regulatory mechanisms to protect red wolves. Finally, the USFWS should enhance recovery by providing information and education about red wolves to hunters and the general public.

KEY WORDS *Canis rufus*, conservation, hunting, mortality, population, red wolf, survival.

Fundamental to management strategies in conservation biology is the connection between sources of mortality and population size (Woodroffe et al. 2007, van de Kerk et al. 2013). Globally, large carnivore species have been subjected to significant anthropogenic mortality, resulting in severe population declines and range contractions (Treves and Karanth 2003, Cardillo et al. 2004, Ripple et al. 2014). As a result, many large carnivores exist as remnant populations requiring legal protections and ongoing conservation to persist in human-dominated landscapes (Linnell et al. 2001, Musiani and Paquet 2004). In particular, intensive predator control programs and excessive hunting reduced red wolves (*Canis rufus*) to a single remnant population along the coastal border of Louisiana and Texas by the mid-twentieth century (Russell and Shaw 1971, Shaw 1975, U.S. Fish and Wildlife Service [USFWS] 1990). This red wolf population was intentionally extirpated from the wild during the 1970s by the USFWS when recovery *in situ* was deemed unlikely because of persecution, disease, poor habitat, and hybridization with coyotes (*Canis latrans*; USFWS 1990, Hinton et al. 2013). Following the development of a captive red wolf breeding program, the USFWS reintroduced wolves into eastern North Carolina, USA during 1987 (USFWS 1990). By 2007, the USFWS reported an increasing proportion of red wolf deaths by anthropogenic sources and suggested that wolf fatalities resulting from gunshots were most problematic to recovery (USFWS 2007, Bartel and Rabon 2013).

Following the reintroduction of red wolves into eastern North Carolina, a population and habitat viability assessment (PHVA) conducted in 1999 predicted annual population growth rate (λ) increases of 20% from 2000 to 2010 with a carrying capacity of 150 individuals in the designated Red Wolf Recovery Area (Kelly et al. 1999). Annual tallies of red wolves fitted with radio-collars and pups counted at dens conducted by the USFWS Red Wolf Recovery Program (Recovery Program) peaked at 131 known individuals in 2001 and then fluctuated between 90 and 125 until 2014 (USFWS 2007, 2014). Because the PHVA reported red wolf hybridization with coyotes to be the primary threat to recovery, the Red Wolf Adaptive Management Plan (RWAMP) was initiated in 2000 to

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prevent coyote introgression into the wild red wolf population (Stoskopf et al. 2005, Rabon et al. 2013, Gese and Terletsky 2015, Gese et al. 2015). However, since 2004, the number of red wolves killed by gunshot increased approximately 2.75 times when compared to years prior to 2004 (Bartel and Rabon 2013). As a result, recent concerns regarding the wild population of red wolves have focused on understanding sources of mortality affecting red wolf population dynamics and their effects on long-term recovery, and potential management strategies to reduce anthropogenic mortality (Sparkman et al. 2011; Hinton et al. 2015*a*,*b*; Way 2014; Murray et al. 2015).

Two previous studies assessed effects of anthropogenic mortality on the reintroduced red wolf population (Sparkman et al. 2011, Murray et al. 2015). Sparkman et al. (2011) suggested that anthropogenic mortality could have additive effects on red wolf populations at low densities, but non-breeding adults in the population could provide density-dependent compensation by replacing breeders that were killed. After reanalyzing the same dataset, Murray et al. (2015) reported that red wolf demographics from 1999 to 2007 were similar to those observed in stationary or increasing wolf populations elsewhere. However, neither study adequately addressed current trends in red wolf survival because they lacked data collected since 2007 when the Recovery Program reported that the average annual number of gunshot-related mortalities had increased significantly (USFWS 2007, Bartel and Rabon 2013). Murray et al. (2015) contended that current conditions were inadequate to establish a viable self-sustaining red wolf population but disagreed with the suggestion of Hinton et al. (2013) for more research to help improve recovery in eastern North Carolina. We suggest that a more comprehensive assessment of red wolf survival is required for several reasons.

First, most anthropogenic mortality was reported to occur during fall and winter, which coincide with the red wolf breeding season (USFWS 2007, Bartel and Rabon 2013). Despite this, Murray et al. (2015) did not assess seasonal variation in red wolf survival. Indeed, Hinton et al. (2015*a*) reported that shooting deaths of red wolves during fall and winter hunting seasons disrupted wolf breeding pairs, allowed coyote encroachment into formerly held wolf territories, and facilitated congeneric pair-bonding between surviving wolves and transient coyotes, which resulted in increased hybridization. Second, Murray et al. (2015) did not account for survival of non-telemetered wolves (e.g., pups). The Recovery Program has cross-fostered captive-born pups into wild litters to augment genetic diversity and growth rates of the wild red wolf population (Bartel and Rabon 2013, Gese et al. 2015) and it is unknown whether captive-born pups had survival rates similar with those born in the wild. Finally, accurate estimates of annual population sizes for red wolves require incorporating recapture rates of pups and age-specific survival rates. To date, these data have not been included in a comprehensive estimate of red wolf population size over time. Therefore, a contemporary assessment of survival, changes in causes of mortality of red wolves over time, and abundance of red wolves in eastern North Carolina is needed to better understand how variation in survival and sources of mortality influence red wolf population size.

The USFWS is responsible for developing recovery plans to address key threats to the survival of endangered species, such as the red wolf (Hoekstra et al. 2002, Treves et al. 2015). Indeed, the Endangered Species Act of 1973 (ESA) requires the USFWS to document factors that imperil species populations, conduct research to determine strategies to eliminate those threats, and then implement those strategies (Scott et al. 2010, Finkelstein et al. 2012). Anthropogenic mortality and hybridization were identified as the 2 primary threats to red wolves (Kelly et al. 1999, USFWS 2007, Rabon and Bartel 2013). Despite measures taken to address hybridization via the RWAMP (Stoskopf et al. 2005, Gese and Terletzky 2015, Gese et al. 2015), the USFWS has not addressed threats of anthropogenic mortality for red wolves. Ultimately, understanding how causes of red wolf mortalities change over time will allow the USFWS to respond with effective management to reduce excessive mortality and achieve population sizes essential to recovery. Our objective was to assess population-level impacts of anthropogenic mortality on the only wild population of red wolves. Specifically, a primary purpose of our analysis was to predict the probability of a given outcome (shooting deaths of red wolves) at a given time (white-tailed deer [*Odocoileus virginianus*] hunting season) for individual wolves. To accomplish this, we assessed monthly and age-class specific survival rates and identified factors influencing the timing and occurrence of mortality.

STUDY AREA

The Red Wolf Recovery Area consisted of a 5-county area (Beaufort, Dare, Hyde, Tyrrell, and Washington) in North Carolina, including 4 national wildlife refuges (Alligator River, Mattamuskeet, Pocosin Lakes, and Swanquarter), a Department of Defense bombing range, and state-owned lands that encompassed about 6,000 km^2 (Fig. 1). Approximately 60–70% of the Recovery Area was privately owned lands comprising agricultural croplands (i.e., corn, cotton, soybean, winter wheat) and managed pine (*Pinus* spp.) forests. Federal and state lands comprised mostly of coastal bottomland forests, pocosin, and fresh and saltwater wetlands (Hinton et al. 2015*c*). Further details of the study area can be found in Hinton and Chamberlain (2010) and Hinton et al. (2015*c*).

METHODS

Field Data Collection

From 1987 to 2013, the Recovery Program annually trapped wild red wolves to fit individuals with mortality-sensitive radio-collars (Teleonics, Mesa, AZ, USA) and regularly monitored radio-marked wolves until individuals died or radio-collars stopped working. Red wolves were captured using padded foot-hold traps (Victor no. 3 Softcatch, Woodstream, Lititz, PA, USA). Detailed life-history data permitted us to assign accurate ages to wolves. Red wolves $\leq$8 months were not typically radio-collared if they were below the minimum physical size to safely wear radio-collars

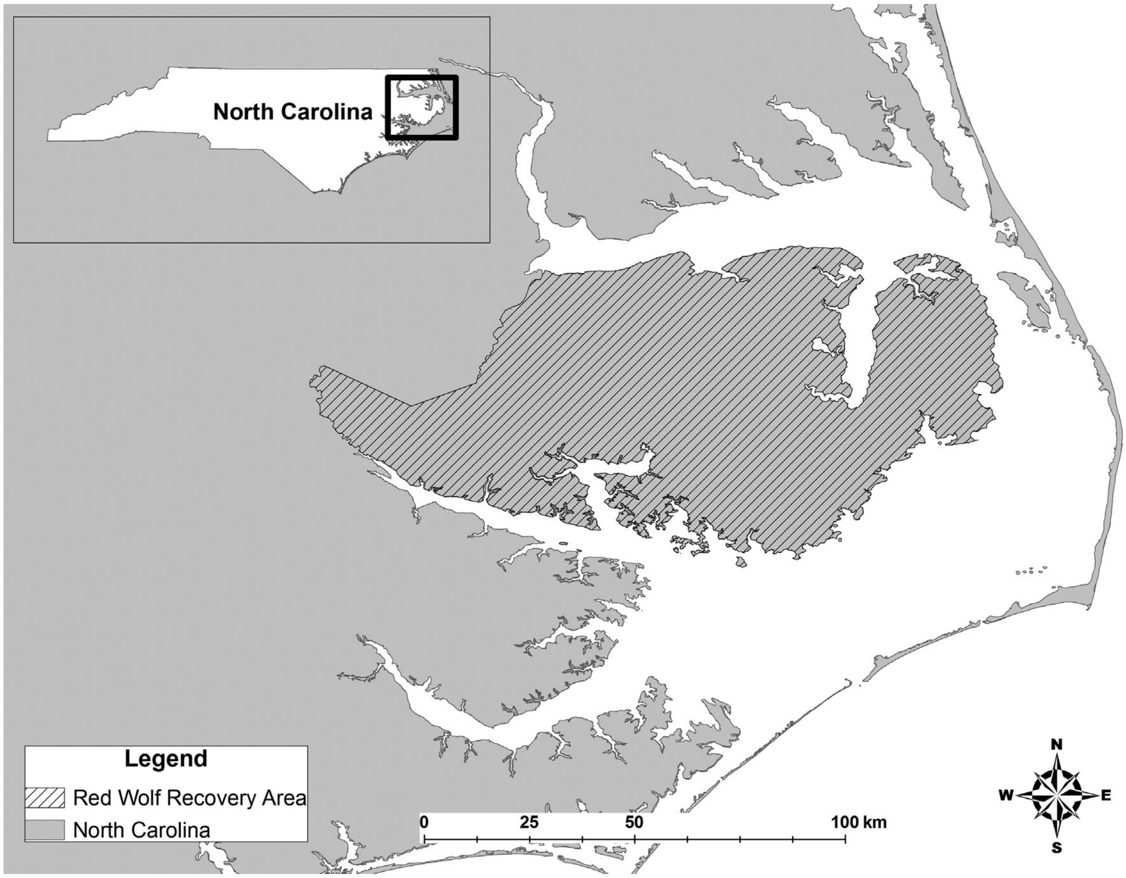

Figure 1. North Carolina, USA, showing the location of the Red Wolf Recovery Area (hatched area) in the eastern portion of the state.

and had the potential to increase in body mass (Hinton and Chamberlain 2010, 2014). Although we used trapping data to accomplish multiple objectives and trapping could not be standardized temporally or spatially, we believe trapping efforts that were part of the large-scale, long-term monitoring efforts conducted across the 5-county Recovery Area provided an adequate proxy for abundance of red wolves in eastern North Carolina (Lovett et al. 2007, Stephens et al. 2015). Furthermore, standardized practices of monitoring the reintroduced red wolf population (RWAMP; Rabon et al. 2013) facilitated data collection in a relatively consistent way to provide the context for interpreting observed changes (Lovett et al. 2007, Gitzen et al. 2012). All methods used to capture and process red wolves were approved by the Louisiana State University Agricultural Institutional Animal Care and Use Committee (Protocol Number AE2009-19) and met guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011).

Recovery Program biologists conducted weekly radio-telemetry flights as their primary means of monitoring radio-collared wolves. This allowed them to identify territories and, during spring, locate dens and daybeds of radio-collared females to count and process pups (Beck et al. 2009, Rabon et al. 2013). From 2000 to 2013, after implementation of the RWAMP, biologists took blood samples of red wolf pups discovered during den checks to verify parentage and maintain a pedigree of the wild population (Miller et al. 2003, Brzeski et al. 2014, Gese et al. 2015) and implanted passive integrated transponder (PIT) tags in each pup subcutaneously to identify non-collared red wolves captured during annual trapping (Beck et al. 2009, Hinton and Chamberlain 2014). Collectively, annual trapping and den work allowed the Recovery Program to estimate population size, survival, and reproduction through a known count approach (USFWS 2007, Rabon et al. 2013).

For radio-collared red wolves, the Recovery Program identified mortality events through detection of a mortality signal during aerial telemetry surveys and recovered carcasses to determine causes of mortality. Recovery Program biologists recorded estimated time of death, suspected or confirmed cause of death, location, and land ownership. If circumstances surrounding the death appeared suspicious and biologists suspected foul play, they contacted USFWS law enforcement officers to collect additional evidence. For law enforcement investigations, wolf carcasses were sent to the USFWS National Forensics Laboratory (Ashland, OR, USA) for necropsy and analysis. For other cases where initial cause of death could not be determined, carcasses were transported to the United States Geological Survey National Wildlife Health Center (Madison, WI, USA) for necropsy. However, citizens occasionally reported road-killed red wolves and wolves mistakenly harvested as coyotes.

We examined capture and processing information, medical history, and mortality reports for each red wolf mortality event from October 1987 to September 2013. We classified mortalities into 3 generalized categories: natural causes (i.e., disease or health-related, intraspecific strife), anthropogenic (i.e., private trapping, vehicle collision, poison, suspected or confirmed gunshot, other suspected illegal killing), or unknown. We classified mortalities as unknown causes of death if there was not enough biomaterial present to determine cause of death (e.g., skeletal remains, hair mat only), necropsy analyses were inconclusive, or multiple causes of death were suspected and not confirmed by necropsy. Mortalities caused by gunshot included suspected cases where there was evidence of foul play (e.g., a cut or removed radio-telemetry collar or bullet wounds), and confirmed cases where there was evidence of bullet fragments through radiographs or necropsy examinations. We confirmed instances of poisoning by necropsy and toxicological analysis. We excluded population monitoring activities (i.e., trapping and den checks) as an anthropogenic source of mortality for 2 reasons. First, deaths caused by population monitoring activities were intermittent, infrequent (4.7% of known deaths), and mostly resulted from faulty genetic testing and euthanizing of hybrids. Second, by not pooling all sources of anthropogenic mortality, we avoided obscuring the relative importance of other anthropogenic sources of mortality (e.g., gunshot, vehicle collisions) with mortalities caused during monitoring efforts. We considered this approach important for interpreting changes in causes of mortality for red wolves because recommendations for reducing anthropogenic sources of mortality caused by gunshots and vehicle collisions are fundamentally different than those reducing mortalities caused by population monitoring. Hereafter, we report percentage of total mortality comprising each of the causes described above.

Cause of Death Analysis

We evaluated changes in causes of mortalities of red wolf carcasses recovered and summarized causes by year. For consistency, we reported mortalities and causes of deaths using October 1 through September 30 as our biological year, similar to the population estimates provided by the USFWS (USFWS 2007). We calculated changes in the number of mortalities of radio-marked red wolves recovered with known causes of death for the entire data series (1987–2013) with logistic regression models using PROC NLMIXED (SAS 9.3, SAS Institute, Cary, NC, USA) in which fixed and random effects were permitted to have a nonlinear relationship to the proportion of red wolf deaths. We considered models with constant, linear, and quadratic time trends, plus we added a mean zero normally distributed random effect of year on the logit scale to explain extra-binomial variation around the trend line to the models. We expected extra-binomial variation (over-dispersion) to occur because logistic regression models are based on an underlying binomial variation. Extra-binomial variation resulted from heterogeneity and the lack of a perfect fit by our model. Therefore, we modeled over-dispersion in our logistic regression models and estimated the proportion of the 3 categories of mortality (i.e., natural, anthropogenic, and unknown) through time. We selected models based on Akaike's Information Criterion for small samples (AIC_c), Akaike weights (w_i), and model deviance (Burnham and Anderson 2002). We compared models including individual covariates to the intercept-only model to determine if the covariates improved fitted models. We considered the model with the lowest AIC_c and the highest model weight as the best model (Burnham and Anderson 2002).

Survival Analyses

We conducted 2 separate survival analyses because the Recovery Program uses 2 types of population surveys to monitor red wolves. Each spring, the Recovery Program monitored radio-collared red wolves associated with breeding territories (USFWS 2007, Gese et al. 2015, Hinton et al. 2015*a*). During spring den checks, Recovery Program biologists located and PIT-tagged red wolf pups in breeding territories by locating daybeds and dens of radio-collared female breeders (Beck et al. 2009, Gese et al. 2015). As a result, the USFWS estimated red wolf population during fall seasons comprised a count of known radio-collared red wolves and known PIT-tagged pups. Therefore, implanting red wolf pups with PIT tags during annual den checks during whelping seasons (Mar–May) allowed Recovery Program biologists to later identify non-collared red wolves during annual trapping efforts throughout the Recovery Area. These mark-recapture encounters served as re-sighting data to estimate annual survival of red wolf pups using a joint live-dead analysis. When PIT-tagged red wolves were radio-collared during annual trapping efforts, individuals were then shifted to the known-fate analysis because routine monitoring provided more frequent radio-telemetry data with higher probabilities of encounters. Telemetry data made it possible to estimate monthly variation in survival of juvenile and adult red wolves.

Known-fate models are commonly used in telemetry studies to estimate survival probability between sampling occasions (White and Burnham 1999, Schwartz et al. 2006, Gusset et al. 2008, Ackerman et al. 2014, Chitwood et al. 2015). For radio-collared red wolves, we calculated survival rate estimates in Program MARK using a parameter estimation analogous to the non-parametric Kaplan–Meier product limit estimator (Kaplan and Meier 1958) through a known-fate approach that employs binomial likelihood functions over a specified interval and allows consideration of individual and external covariates (White and Burnham 1999). Our known-fate model assumed that the process of radio-collaring red wolves did not affect individual fates, that fates among individuals were independent, that the encounter probability was equal to 1, and that censoring was unrelated to mortality (White and Burnham 1999). The basic model used in our survival analysis was a logistic model with a logit link. We defined October 1987 as the time of origin of the study to obtain survival estimates.

Radio-telemetry flights were scheduled to occur twice a week to monitor radio-collared red wolves. However, inclement weather and other logistical constraints prevented monitoring wolves for extended periods each year. Indeed, many red wolves were not found for greater than 2 weeks at a time, and this introduced biases into our analysis as described in Heisey et al. (2007). When time of death is not estimated exactly, many tied death times result in the data, and estimates are no longer valid. Therefore, we followed the suggestion of Heisey and Patterson (2006) and used methods for interval-censored data. The use of monthly intervals accommodated the lack of information on exact time of death and provided unbiased estimates of monthly and annual survival.

We summarized capture data for all red wolves during 1987–2013 into monthly encounter histories based on White and Burnham's (1999) live-dead encounter format for entry into Program MARK. This allowed for staggered data entry of new red wolves and right-censoring of individuals to a month when they were lost because of radio failure or other reasons (Pollock et al. 1989, White and Garrott 1990). We used data from censored individuals in the model up until the time of censoring. Although cause of death for an individual red wolf was not always known, knowing the interval in which the animal died allowed us to use a known-fate model (White and Burnham 1999). In cases where individuals were not encountered during a subsequent interval, we estimated time of morality as the midpoint between encounters. We recorded red wolves as alive, dead, or censored for each monthly interval.

We investigated the influence of individual and temporal covariates on survival of radio-collared red wolves with all possible models developed from combinations of year, month, age, and sex. Structure for all models was additive, with no interaction terms. We treated each year as an attribute group in Program MARK, and estimated annual survival as the product of the 12 monthly survival estimates. We included age and sex as individual covariates to investigate the potential influence of these factors on survival. Temporal covariates included year and month. We included month as a categorical effect and used December as the reference category. We evaluated model sets using AIC_c. We considered the model with the smallest AIC_c and the largest Akaike weights (w_i) to be the most parsimonious. We did not conduct goodness-of-fit tests because known-fate data types can be fit as a completely saturated model leaving no degrees of freedom. The global model considered in our survival analysis was also the saturated model and no goodness-of-fit test was possible because the saturated model left no degrees of freedom (Schwartz et al. 2006). We calculated the relative deviance as the difference in −2log (likelihood) of the current model and −2log of the saturated model, in which the deviance is a measure of the relative goodness of fit of each model (White and Burnham 1999).

For non-collared red wolves marked with PIT tags, we used the Burnham joint live-dead model in Program MARK to estimate survival rates until recapture from their first year through their fourth year of age (Burnham 1993, White and Burnham 1999). Individuals entered our analysis via 1 of 3 origins: wild born, cross-fostered, and released. Most wild born red wolves were encountered as pups in dens and then marked with PIT tags. During annual trapping, wild born red wolves were encountered a second time when fitted with radio-collars. First encounters for wild born red wolves not discovered as pups in dens occurred during annual trapping when non-PIT tagged juveniles and adults were captured, marked with PIT tags, and fitted with radio-collars. During the initial phase of reintroduction, captive-born adult red wolves and their pups (<6 months) were released from island propagation sites into the wild (Phillips et al. 2003). However, after the RWAMP was implemented in 2000, captive-born red wolf pups were cross-fostered into wild litters (Gese et al. 2015). In both situations, first encounters occurred when pups were PIT tagged and introduced into the wild. Like wild-born pups, second encounters for released and cross-fostered pups occurred during annual trapping efforts when they were recaptured and fitted with radio-collars. When red wolf pups were recaptured and radio-collared, they were entered into the known-fate model described above.

With the Burnham joint live-dead model, both live encounters and dead recoveries are used to estimate survival. We set the site fidelity parameter (F) to 1 for all models (i.e., no emigration from the study area). From the minimum AIC_c model, we obtained age-specific survival estimates (0–1 and >1 years of age) for the combined origins. Using these survival estimates, we constructed the probability of a red wolf living 1, 2, 3, and 4 years after being born, fostered, or released into the wild population. The probability of surviving to 1 year of age was the first-year survival estimate ($\hat{S}_1$). The probability of survival to year 2 was the product of the first- and second-year survival ($\hat{S}_1\hat{S}_2$). The probability of survival to year 3 was the product of the first-year survival and the second-year survival squared to provide a 3-year estimate ($\hat{S}_1*(\hat{S}_2^2)$), and similarly for the fourth-year probability ($\hat{S}_1*(\hat{S}_2^3)$). We computed the variances of these survival estimates with the delta method using the formula below (age $k = 0, 1, 2, 3$), and used the covariances of these estimates because the model providing the estimates had a sampling covariance between the estimates.

$$\mathrm{Var}(\hat{S}_1\hat{S}_2^k) = \hat{S}_2^{2(k-1)}\left(2k\hat{S}_1\hat{S}_2\mathrm{Cov}(\hat{S}_1,\hat{S}_2) + k^2\hat{S}_1^2\mathrm{Var}(\hat{S}_2) + \hat{S}_2^2\mathrm{Var}(\hat{S}_1)\right)$$

$$\mathrm{SE}(S_1S_2^k) = \sqrt{\mathrm{Var}(S_1S_2^k)}$$

We estimated the population of pups that remained after 4 years by first determining the number of pups released in a particular year minus the number with known fate that were removed each year, either through capture and marking with radio-collars, or else recovered dead. To estimate fate of pups with unknown status, we applied the probability of survival to estimate number of these unknown pups remaining alive at each year:

$$L_1 = n_4\hat{S}_1, L_2 = n_3\hat{S}_1\hat{S}_2, L_3 = n_2\hat{S}_1\hat{S}_2^2, \text{ and } L_4 = n_1\hat{S}_1\hat{S}_2^3$$

where L_a were the number of pups of age $a = 1, \ldots, 4$, from years $4, \ldots, 1$, with number of unknowns n_4, n_3, n_2, and n_1, respectively. We computed the standard error of the estimated population of pups with unknown fates for each year as

$$\begin{aligned}\mathrm{SE}(L_1 + L_2 + L_3 + L_4) = {} & [2\hat{S}_1(3n_1\hat{S}_2^2 + 2n_2\hat{S}_2 + n_3) \\ & (n_1\hat{S}_2^3 + n_2\hat{S}_2^2 + n_3\hat{S}_2 + n_4)\mathrm{Cov}(\hat{S}_1, \hat{S}_2) \\ & + (n_1\hat{S}_2^3 + n_2\hat{S}_2^2 + n_3\hat{S}_2 + n_4)^2\mathrm{Var}(\hat{S}_1) \\ & + \hat{S}_1^2(3n_1\hat{S}_2^2 + 2n_2\hat{S}_2 + n_3)^2\mathrm{Var}(\hat{S}_2)]^{1/2}\end{aligned}$$

We investigated the influence of individual and temporal covariates on survival of non-collared red wolves with a set of candidate models developed from all combinations of survival (S), age (a), origin (g), probability of carcass recovery (r), recapture probability (p), time-specific survival (t), and constant survival (.). We evaluated model sets using AIC$_c$. We considered the model with the smallest AIC$_c$ and the largest Akaike weights (w_i) to be the most parsimonious. Because the global model considered in our survival analysis was also the saturated model, no goodness-of-fit test was possible (Schwartz et al. 2006).

Annual Population Sizes and Growth Rates

The USFWS used combined counts of PIT-tagged pups and radio-collared individuals to estimate annual sizes of the wild population. Obviously, not all red wolves were accounted for because not all pups were found or recaptured. These individuals were usually radio-collared as juveniles and adults during subsequent annual trapping efforts, but some were never captured. Therefore, we used Burnham live-dead models to provide a more accurate estimate of population size by calculating the survival rates of PIT-tagged pups. Specifically, we first determined the number of pups PIT tagged in a particular year and then used probabilities of pups being alive 1, 2, 3, and 4 years after release to apportion them out across the 4-year period. We then subtracted the number of PIT-tagged wolves radio-collared or recovered dead for each year. This left the red wolves that were of an unknown status. We then applied the probability of survival estimates from the Burnham live-dead models to determine the number of unknowns remaining alive each year. We added the number of unknowns estimated to be alive for a given year into the radio-collared population to obtain the population estimate. The standard error of the population estimate for each year was the product of the standard error for unknown red wolves and the probability of surviving to that year. Therefore, the standard error of the population estimate for each year was the same as the standard error of unknowns remaining because the number of living radio-collared wolves was known without error (i.e., it had no variance). We reported standard errors only for 2000–2013 because more thorough attempts to find and investigate dens to construct a red wolf pedigree began in 2000 (Miller et al. 2003, Brzeski et al. 2014, Gese et al. 2015). In other words, accurate estimates of recapture rates for non-collared red wolves occurred after the implementation of the RWAMP when finding and marking red wolves and monitoring breeding pairs became essential to limiting hybridization.

Table 1. Model selection results from the cause-specific mortality analysis for evaluating anthropogenic mortality as a proportion of total mortalities with known cause of death in red wolves in eastern North Carolina, USA, 1987–2013. For each model, we provide Akaike's Information Criterion (AIC$_c$), Akaike weights (w_i), number of estimable parameters (K), and deviance.

Model	AIC$_c$	ΔAIC$_c$	K	w_i	Deviance
Trend	104.91	0.00	2	0.46	100.39
Trend + random effect	105.61	0.70	3	0.33	98.52
Trend^2	107.46	2.55	3	0.13	100.38
Trend^2 + random effect	108.38	3.47	4	0.08	98.48
Constant + random effect	113.44	8.53	2	0.01	108.92
Constant	124.34	19.43	1	0.00	122.17
Year	1,510.02	1,405.11	26	0.00	54.02

We compiled annual estimates of population size by year (1 Oct–30 Sep) from 1987 through 2013 by summing the number of known radio-collared wolves with the number of estimated non-collared wolves remaining alive each year. We then used our estimates of population size to calculate annual population growth rate (λ) for year n by dividing the estimated population size in the year n+1 by the population size in year n.

RESULTS

From 1987 and 2013, we recorded 372 red wolf deaths and identified cause of death for 300 (80.6%) of these wolves. Anthropogenic causes of death accounted for 73% of red wolf mortality, whereas natural causes comprised 27%. Of 219 human-caused deaths, 51% involved foul play ($n = 112$), including gunshot ($n = 88$), poison ($n = 11$), and other suspected illegal killings ($n = 13$). The proportion of mortality attributable to anthropogenic causes increased over time (Wald $\chi^2_1 = 20.47$, $P < 0.001$; Table 1 and Fig. 2). We also observed an increasing trend of red wolf mortalities attributed to gunshot over time (Wald $\chi^2_1 = 13.96$, $P < 0.001$; Table 2 and Fig. 3). Vehicle collisions, capture by private

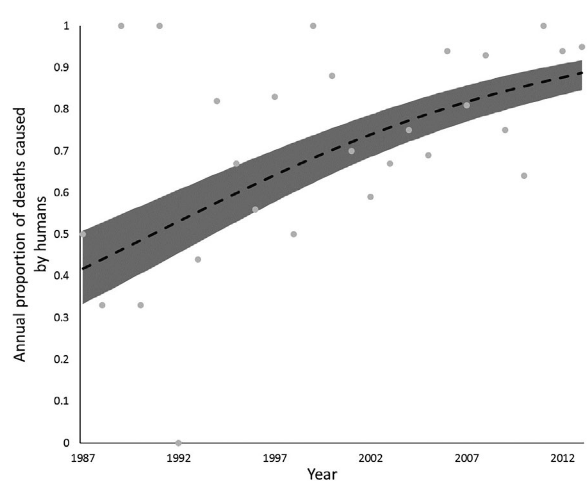

Figure 2. Proportion of red wolf mortalities caused by humans relative to overall mortality in eastern North Carolina, USA, 1987–2013. Observed values and 95% confidence limits are represented by circles and the gray shaded area, respectively.

Table 2. Model selection results from the cause-specific mortality analysis for evaluating gunshot mortality as a proportion of anthropogenic mortalities over time for red wolves in eastern North Carolina, USA, 1987–2013. For each model, we provide Akaike's Information Criterion (AIC_c), Akaike weights (w_i), number of estimable parameters (K), and deviance.

Model	AIC_c	ΔAIC_c	K	w_i	Deviance
Trend	70.56	0.00	2	0.74	66.04
Trend^2	72.64	2.08	3	0.26	65.55
Trend^2 + random effect	83.53	12.97	4	0.00	73.63
Trend + random effect	88.04	17.48	3	0.00	80.95
Constant	88.78	18.22	1	0.00	86.62
Constant + random effect	91.07	20.51	2	0.00	86.54
Year	1,509.04	1,438.48	26	0.00	53.04

Table 3. The top 5 candidate models and null model {$S(.)$} from the known-fate analysis used to model survival (S) of radio-collared red wolves in eastern North Carolina, USA, 1987–2013. For each model, we provide the change in Akaike's Information Criterion (ΔAIC_c), Akaike weights (w_i), number of estimable parameters (K), and the deviance.

Model	K	AIC_c	ΔAIC_c	w_i	Deviance
S(month + age^2)	14	2,975.32	0	0.99	2,947.27
S(month)	12	2,992.29	16.97	0.01	2,968.25
S(month + sex)	13	2,993.35	18.02	0.00	2,967.30
S(age^2)	3	2,993.83	18.51	0.00	2,987.83
S(month + age)	13	2,994.22	18.90	0.00	2,968.17
S(.)	1	3,015.64	40.32	0.00	3,013.64

trappers, and management-related activities accounted for 34%, 8%, and 7% of red wolf mortalities attributed to anthropogenic causes, respectively. Health-related cases accounted for 70.4% of natural causes of death, whereas intraspecific strife accounted for 29.6%.

From 19 to 2013, 537 red wolves were radio-collared. Demographic data were available for 365 of 372 observed red wolf mortalities and included 72 pups, 95 juveniles, and 198 adults. Our analysis indicated that month and age were the 2 most important factors influencing red wolf survival, whereas year and sex were not important (Tables 3 and 4). The estimated average age at time of death was 3.2 years; only 9 wolves survived past age 10. Mean monthly survival rates were lowest from October through December (Fig. 4). Age-specific annual survival rates ranged between 0.14 and 0.81 (Fig. 5). Maximum annual survival occurred at age 5 (0.81), and 68% of red wolves died before age 4.

From 1987 to 2013, the annual probability of recapturing and radio-collaring previously PIT-tagged red wolf pups was 62% ($n = 826$). Only 18 carcasses of non-collared red wolves (18 wild born) were recovered; there were never any carcasses recovered for fostered pups. Three carcasses of released pups were recovered. Of the candidate models, survival estimated as a function of 2 age classes (pups and ages 2–4 combined) was our top model (Tables 5 and 6). We considered this the most plausible model because few red wolves survived to 4 years of age without being recaptured and fitted with radio-collars, so there were little data to estimate separate survival rates for 3- and 4-year-old wolves without radio-collars. Further, assuming constant survival after the first year is biologically reasonable and simplifies the computation of the number of non-collared red wolves remaining alive in the wild population. Mean estimates for first-year pup survival ($\hat{S}$) calculated by year ranged 0.505–0.721 and mean survival was 0.619 ± 0.056 for the entire study period. For red wolves that survived their first year (ages 2–4), mean survival by year ranged between 0.218 and 0.531 and mean survival was 0.360 ± 0.083. Within the top model, recapture probability (p) was constant across origin (i.e., wild born, fostered, released) and ages, whereas the probability of recovering dead (r) differed by origin. The main reason that survival estimates required a group effect was because there were never any dead recoveries for the fostered group. Although sample sizes for fostered and released individuals were smaller than those born in the wild, we detected no differences in survival among wild born, fostered, and released wolves.

Red wolf population estimates generally increased through time, peaking in 2005–2006 and then decreasing from 2007

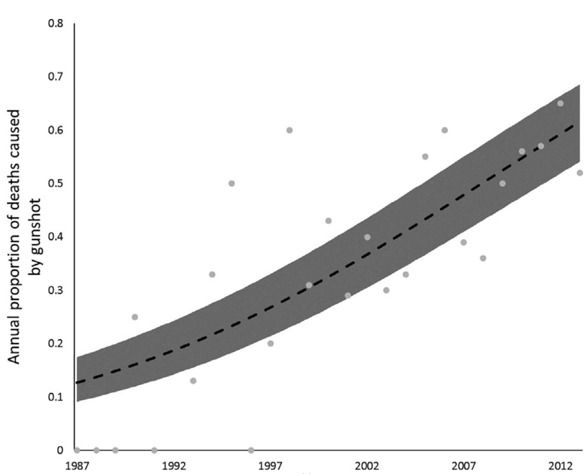

Figure 3. Proportion of red wolf mortalities caused by gunshot relative to overall mortality in eastern North Carolina, USA, 1987–2013. Observed values and 95% confidence limits are represented by circles and the gray shaded area, respectively.

Table 4. Summary of results from the best model in the known-fate analysis of survival for radio-collared red wolves, North Carolina, USA, 1987–2013. Month was a categorical variable and December was the reference category. Shown are β coefficients, standard error (SE), 95% upper confidence interval (UCI), and 95% lower confidence interval (LCI).

Parameter	β	SE	UCI	LCI
Intercept	2.82	0.17	3.16	2.48
Jan	0.66	0.26	1.17	0.15
Feb	0.59	0.25	1.08	0.09
Mar	1.04	0.29	1.62	0.47
Apr	0.67	0.26	1.18	0.16
May	0.40	0.24	0.86	−0.07
Jun	0.85	0.28	1.39	0.31
Jul	1.01	0.29	1.58	0.43
Aug	1.02	0.29	1.59	0.44
Sep	0.79	0.27	1.32	0.26
Oct	0.19	0.23	0.64	−0.25
Nov	0.06	0.21	0.48	−0.36
Age	0.28	0.06	0.40	0.16
Age^2	−0.03	0.01	−0.02	−0.04

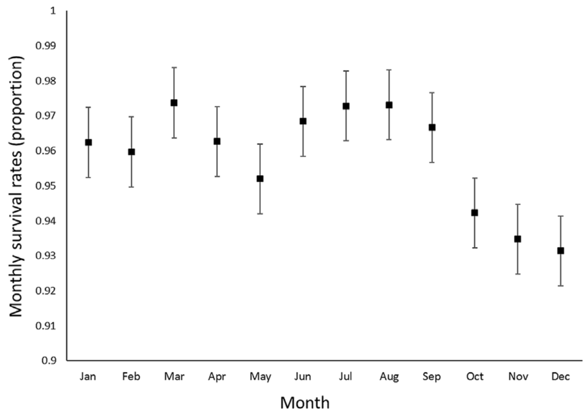

Figure 4. Mean monthly survival rates of red wolves in eastern North Carolina, USA, 1987–2013, indicating survival declines precipitously from October through December. The 95% confidence limits are represented by the error bars.

to 2013 (Fig. 6). Overall, annual growth rates (λ) ranged between 0.78 and 2.07 (Fig. 7). From 1998 to 2005, the red wolf population increased from an estimated 90 to 151 wolves with an average annual λ of 1.12. However, from 2005 to 2013, the red wolf population decreased from an estimated 151 to 103 wolves with an average annual λ of 0.96.

DISCUSSION

Recently, Murray et al. (2015) reported that gunshots were consistently responsible for approximately 25% of red wolf deaths from 1999 to 2014, and detected no effect of age on red wolf survival from 1999 to 2007. However, our findings indicate that the proportion of red wolf deaths caused by gunshot increased significantly after 1999, survival rates were lowest during fall and winter hunting seasons, and younger red wolves were more susceptible to gunshot mortalities. From 2000 to 2013, gunshots comprised 42% of identified causes of red wolf deaths and the annual proportion of wolf deaths caused by gunshot increased from approximately 25% to 60% (Fig. 3). Our findings differ from those of Murray et al. (2015) because their analysis compared mortalities evaluated through examination of data from 1999 to 2007 to summaries reported in USFWS quarterly and annual progress reports during 2008–2014 (USFWS 2016), whereas our study was a consistent analysis of actual field data from 1987 to 2013. We suggest that our estimates of population size, survival, and patterns of mortality are more robust and detailed than previous assessments because of the inclusion of data collected since 2007.

Corresponding with the North Carolina fall and winter hunting seasons, monthly survival rates for red wolves were lowest during October–December (Fig. 4). Although mortality rates were greatest for younger red wolves, we observed no difference in survival between captive-born and wild-born wolves; 68% of monitored wolves died before age 4 regardless of their origin. During the past 2 decades, the coyote population has increased in eastern North Carolina and they are subject to intensive control efforts via shooting and trapping (Way 2014; Hinton et al. 2015*a*,*b*). Despite

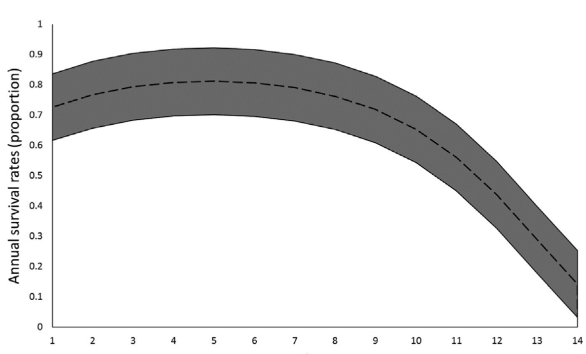

Figure 5. Annual age-specific survival rates of red wolves in eastern North Carolina, USA, 1987–2013. The 95% confidence limits are represented by the shaded area.

Table 5. Models considered for the survival analysis of non-collared red wolves in North Carolina, USA, 1987–2013, using the Burnham joint live-dead model in Program MARK. For each model, we provide Akaike's Information Criterion (AIC_c), the change in Akaike's Information Criterion (ΔAIC_c), Akaike weights (w_i), number of estimable parameters (K), and deviance. Model selection notation follows White and Burnham (1999). S = probability of survival; a = number of age classes; g = origin (wild born, fostered, and released); r = probability of recovering dead; p = recapture probability, and F = probability of remaining in the sampling area fixed to 1.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
$\{S(a2+g)\ p(.)\ r(g)\ F=1\}$	1,225.08	0.00	0.19	8	822.86
$\{S(a2)\ p(.)\ r(g)\ F=1\}$	1,225.33	0.25	0.17	6	827.22
$\{S(a3+g)\ p(.)\ r(g)\ F=1\}$	1,225.45	0.37	0.16	9	821.17
$\{S(a3)\ p(.)\ r(g)\ F=1\}$	1,225.58	0.50	0.15	7	825.42
$\{S(.)\ p(.)\ r(g)\ F=1\}$	1,225.60	0.52	0.14	5	829.52
$\{S(g)\ p(.)\ r(g)\ F=1\}$	1,226.18	1.10	0.11	7	826.02
$\{S(a4)\ p(.)\ r(g)\ F=1\}$	1,227.55	2.48	0.06	8	825.34
$\{S(g)\ p(g)\ r(g)\ F=1\}$	1,229.26	4.18	0.02	9	824.98
$\{S(.)\ p(.)\ r(.)\ F=1\}$	1,229.62	4.54	0.02	3	837.62
$\{S(g)\ p(.)\ r(.)\ F=1\}$	1,230.17	5.09	0.02	5	834.10
$\{S(g)\ p(g)\ r(.)\ F=1\}$	1,233.22	8.14	0.00	7	833.05

Table 6. Parameter estimates obtained from the best model in the Burnham joint live-dead analysis of survival (S) for non-collared red wolves, North Carolina, USA, 1987–2013. Shown are β coefficients, standard error (SE), 95% upper confidence interval (UCI), and 95% lower confidence interval (LCI).

Parameter[a]	β	SE	UCI	LCI
$S_{\text{age 1}}$	−0.75	0.71	0.64	−2.13
$S_{\text{age 2}}$	−1.81	0.86	−0.13	−3.49
S_{wild}	1.24	0.72	2.65	−0.18
S_{fostered}	1.66	0.84	3.30	0.01
p	0.78	0.29	1.35	0.22
r_{wild}	−2.71	0.24	−2.23	−3.19
r_{fostered}	−17.11	1,684.74	3,284.99	−3,319.21
r_{released}	−0.51	0.73	0.92	−1.94

[a] $S_{\text{age 1}}$ = survival for pups; $S_{\text{age 2}}$ = survival for ages 2–4; S_{wild} = survival for wild born pups; S_{fostered} = survival for fostered pups; p = recapture probability; r_{wild} = probability of recovering dead wild born pups; r_{fostered} = probability of recovering dead fostered pups; r_{released} = probability of recovering dead released pups.

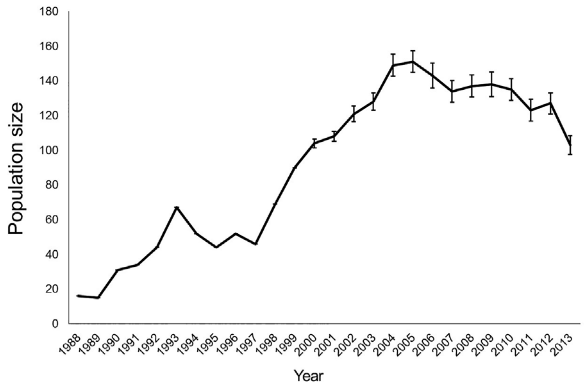

Figure 6. Estimated annual population sizes of red wolves in eastern North Carolina, USA, 1987–2013. Error bars indicate standard errors. Standard errors were reported only for 2000–2013 because after 1999 dens were investigated more thoroughly to sample blood from pups each spring to verify and construct a red wolf pedigree (Miller et al. 2003). Standard errors represent unknown red wolves in the wild population.

being the larger of the 2 species, shooting deaths of red wolves typically occurred when hunters confused wolves for coyotes (Hinton et al. 2013, 2015*a*,*b*; Newsome et al. 2015). In particular, red wolf pups during fall are not fitted with radio-collars, are similar to coyotes in body size (Hinton and Chamberlain 2014), and are more likely to be misidentified by hunters as coyotes. Consequently, we likely underestimated pup mortality caused by shootings because pups were not radio-monitored and their mortalities may have gone undetected.

Decreased survival rates in October–December are not surprising considering other studies that observed significant declines in eastern coyote survival during fall and winter hunting seasons (Chamberlain and Leopold 2001, Van Deelen and Gosselink 2006). Van Deelen and Gosselink (2006) reported coyote survival declined precipitously during fall when harvest of agricultural crops coincided with hunting seasons, when inexperienced juvenile coyotes were more susceptible to opportunistic killing by hunters. Similarly, approximately 30% of the Recovery Area comprised agricultural fields where agricultural activities influenced availability of vegetative cover for red wolves

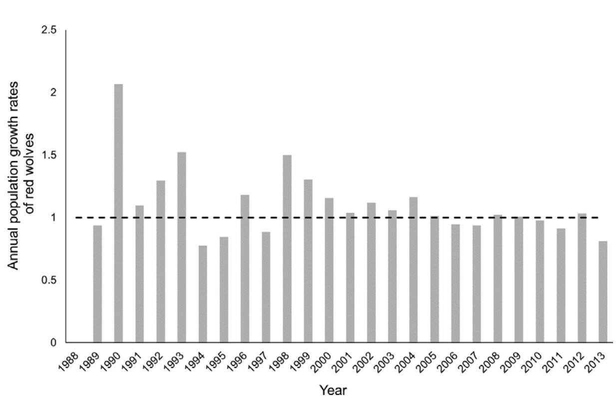

Figure 7. Estimated annual growth rates of red wolves in eastern North Carolina, USA, 1987–2013.

(Chadwick et al. 2010, Hinton and Chamberlain 2010, Dellinger et al. 2013). Harvest of agricultural crops occurred just prior to fall and winter hunting seasons, and extensive loss of vegetative cover reduced refugia for red wolves during a period of elevated human activity. Younger red wolves likely suffered greater mortality than adults during this time for 2 reasons. First, juveniles typically disperse from their natal areas between September and March (Karlin and Chadwick 2012) and are at greater risk of encountering hunters in areas unfamiliar to them. Second, red wolf pups encounter significant decreases in availability of vegetative cover and increases in human activity for the first time.

During 1999, when the red wolf population was estimated by the Recovery Program to comprise approximately 80 individuals, the PHVA predicted the wild population would increase 20% each year from 2000 to 2010 and reach a carrying capacity of approximately 150 individuals (Kelly et al. 1999). Our population estimates tracked the PHVA projections until 2005, when the red wolf population peaked at an estimated 151 individuals. Since 2005, the population has steadily declined to about 103 individuals in 2013. Although numbers of mortalities were generally consistent across years, causes of death have changed. Previously, Phillips et al. (2003) noted that most mortalities of red wolves resulted from accidental (i.e., vehicle strike) or natural (i.e., intraspecific strife) causes. Since 2002, the proportion of mortalities resulting from vehicle collisions has declined and gunshots are now the leading cause of death.

The 2007 USFWS 5-year review noted that the red wolf population was increasing with stable recruitment and adult survival, but documented the initial 2006 decline corresponding with an increase in shooting deaths. Notably, since 2004, the number of red wolves killed by gunshot has increased approximately 2.75 times when compared to years prior to 2004 (Bartel and Rabon 2013). Additionally, the wild population experienced a gradual decline in annual growth rates since 2004 (Fig. 7). Our survival models indicated no change in survival rate of red wolves over time (i.e., no year effect), indicating that the population declined despite no change in yearly survival rates. Some compensatory mechanisms are likely operating within the red wolf population because the increase in anthropogenic mortality coincided with a similar decrease in the occurrence of natural mortality, and compensatory processes are routinely documented (Sinclair and Pech 1996, Péron 2012). However, because red wolves and coyotes are capable of hybridizing, we suggest that reproductive interference by coyotes may explain how the wolf population could decline despite no change in yearly survival rates (Mallet 2005, Gröning and Hochkirch 2008). Hinton et al. (2015*a*) reported increased occurrence of coyote encroachment and replacement of resident red wolves after resident wolf breeders were killed by humans. Consequently, when no red wolf mates were available, surviving resident wolves paired with coyotes creating congeneric breeding pairs responsible for hybridization. Indeed, hybridization was considered a primary threat to the persistence of the wild population and, in response, the RWAMP was developed and implemented to prevent coyote introgression via sterilization of coyotes paired with red wolves (Stoskopf et al. 2005, Hinton et al. 2013, Gese and Terletzky 2015, Gese et al. 2015). Regardless of whether coyote mates are fertile or sterile, congeneric pairings with coyotes represents lost reproductive effort by the red wolf population (Brzeski et al. 2014, Hinton et al. 2015*a*). Despite no change in annual survival rates, pairings between surviving red wolf mates with encroaching coyotes prevented wolf compensation of losses to anthropogenic mortalities via reproduction. The Recovery Program likely softened the decline in population size and annual growth rates of the wild red wolf population via intensive management (i.e., replacing sterilized non-wolf placeholders with wolves; Gese and Terletzky 2015) and annual augmentation with captive-born wolves (Bartel and Rabon 2013, Gese et al. 2015). Regardless, human activities, either intentional (i.e., gunshot) or not (i.e., vehicle collision), have become the leading cause of mortality for wild red wolves and are affecting size and annual growth of the wild population.

Anthropogenic mortality was ultimately responsible for the extirpation of red wolves and continues to limit growth of the reintroduced population. Hinton et al. (2013) suggested that increased research was necessary to tally general threats to red wolves and ultimately understand mechanisms that could facilitate a stable red wolf population in eastern North Carolina. Murray et al. (2015) disagreed with this suggestion by asserting that the RWAMP provided red wolves with conditions allowing them to survive and produce young. They believed conditions in eastern North Carolina were inadequate to establish a sustainable red wolf population, and asserted that research suggested by Hinton et al. (2013) could only prove valuable in the broader context of wolf colonization in eastern North America and endangered species recovery. Although the RWAMP was successful in limiting coyote introgression (Gese and Terletzky 2015, Gese et al. 2015), it was not successful in providing conditions favorable for red wolf survival. This is evident when considering that shooting deaths of red wolves were correlated with a significant increase in breeding pair disbandment (Sparkman et al. 2011, Hinton et al. 2015*a*), disruption of wolf packs (Bohling and Waits 2015, Hinton et al. 2015*a*), and facilitation of coyote encroachment and hybridization (Bohling and Waits 2015; Hinton et al. 2015*a*,*c*) simultaneous with the decline in annual red wolf population size and growth rates reported herein. The RWAMP was implemented in 2000 to establish a framework to limit hybridization between red wolves and coyotes (Stoskopf et al. 2005, Gese et al. 2015), not to address factors affecting red wolf survival such as excessive anthropogenic mortality (Way 2014; Hinton et al. 2015*a*,*b*). Therefore, we suggest site-specific research focused on evaluating ways to minimize threats is fundamental to understand how survival and population sizes are expected to change as red wolves experience deteriorating conditions. Specifically, we suggest further studies are needed to better understand how anthropogenic factors disrupt mechanisms that facilitate stable and reproductively isolated red wolf populations (Fredrickson and Hedrick 2006; Hinton et al. 2013, 2015*a*; Fredrickson 2016). This is crucial for the USFWS to respond to threats with effective management and promote recovery of the eastern North Carolina population as mandated by the ESA (Scott et al. 2010, Finkelstein et al. 2012).

MANAGEMENT IMPLICATIONS

Mortalities of red wolves via gunshot that occur during hunting seasons will have to involve regulation of coyote hunting to prevent intentional and accidental killing of red wolves. A court-approved settlement agreement between the North Carolina Wildlife Resources Commission (NCWRC) and environmental groups appears to be the first step in developing an effective management policy designed to reduce anthropogenic mortality (Red Wolf Coalition; Defenders of Wildlife; and Animal Welfare Institute vs. North Carolina Wildlife Resources Commission; Gordon Myers, Executive Director, North Carolina Wildlife Resources Commission 2014). For example, 10 fewer red wolves were killed via gunshot during the 2 years following the settlement than the preceding 2 years (7 vs. 17 shooting deaths). To reduce negative effects of anthropogenic mortality and ensure long-term persistence of red wolves, the USFWS will need to re-implement previous long-standing and proven management practices on public and private lands (e.g., Red Wolf Adaptive Management Plan), define conditions for when wolves will be removed from recovery areas, implement more effective management strategies to address wolves causing such conditions, and cease issuing take permits as a first line response to dealing with said wolves (USFWS 2016). Equally as important, the USFWS should establish an effective management response to mitigate gunshot mortality through stronger regulation of coyote hunting, develop or revise regulatory mechanisms that are ecologically and biologically supported to protect red wolves. Finally, the USFWS can improve public perception of red wolves and mitigate anthropogenic factors negatively affecting recovery through tailored education and outreach programs for hunters and the general public.

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