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LETTER

The Challenges of Red Wolf Conservation and the Fate of an Endangered Species Recovery Program

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Abstract

Endangered red wolves (*Canis rufus*) receive intense conservation efforts in the United States, and to date, population recovery has been challenged by hybridization with closely related coyotes (*C. latrans*) and illegal human-caused mortality. Ongoing review of the red wolf program in the single recovery area in North Carolina prompted us to compare demography (survival, recruitment) and cause of death of red wolves and coyotes/hybrids. In most respects, canids had similar demographic rates, although sterilization was effective in controlling coyote reproduction. Comparison of previous (1999-2007) to contemporary (2009-2014) causes of death revealed that shooting mortality consistently accounted for ~25% of wolf mortality. As evidenced by the lack of coyote deaths from strife with wolves, and stationary/declining wolf numbers during the last 15 years, current conditions are inadequate to establish a viable self-sustaining wolf population. Accordingly, the program review should determine whether: (1) banning coyote hunting will sufficiently benefit wolf survival or recruitment; (2) the wolf population should be considered conservation-reliant under revised recovery goals; or (3) the recovery program in North Carolina should be abandoned.

Introduction

The red wolf (*Canis rufus*) has had longstanding controversy over its taxonomy, and at different times was recognized as a distinct species, a subspecies of gray wolf (*C. lupus*), a hybrid between coyote (*C. latrans*) and gray wolf, or a conspecific group with eastern wolf (*C. lycaon*; Murray & Waits 2007). Through time, red wolf taxonomy endured attempts at clarification, including via morphological, ecological, and genetic analyses seeking to distinguish closely related canid groups. The red wolf debate persists today despite the advent of sophisticated genomic tools for reconstructing canid evolutionary history (von Holdt *et al.* 2011). Indeed, while the primary authority on mammalian taxonomy considers red wolf as conspecific with gray wolf (Wozencraft 2005), the International Union for the Conservation of Nature (IUCN) provisionally recognizes red wolves as a distinct species having critically endangered status (Kelly *et al.* 2008). Similarly, red wolf is listed as endangered in the United States, and as part of federal responsibility over endangered species, it is subject to intensive recovery efforts directed at reestablishment of a viable population in the wild (USFWS 1989, 2007).

In 1987, the U.S. Fish and Wildlife Service (USFWS) initiated an experimental, nonessential release of captive-bred red wolves in a recovery area in eastern North Carolina (Figure 1). Initially, the area was chosen because coyotes were thought to be absent, but by the early 1990s coyotes were known to be present and had interbred with wolves (Phillips *et al.* 2003; Adams *et al.* 2007). By the late 1990s a population and habitat viability assessment identified hybridization as a primary threat to red wolf recovery (SSC/IUCN 1999), leading to a Red Wolf Adaptive Management Plan (RWAMP) designed to reduce or eliminate this threat (Kelly 2000; USFWS 2009–2013). The RWAMP assumes sterilized coyotes/hybrids will hold space until wolves can colonize territories vacated by

Figure 1 Historic range of the red wolf as recognized by the U.S. Fish and Wildlife Service (USFWS 1990), and the red wolf recovery area in eastern North Carolina.

selective removal, with wolves eventually excluding coyotes/hybrids naturally through competitive exclusion and strife. The RWAMP involves: (1) capture and sterilization of coyotes and hybrids; (2) strategic euthanasia of sterilized coyotes/hybrids; (3) insertion or natural dispersal of wolves in areas recently vacated by euthanized coyotes/hybrids; and (4) opportunistic cross-fostering of captive-born wolf pups by wild red wolves. The program is supported by intensive efforts to monitor demography and behavior of free-ranging canids in the recovery area (USFWS 2007). Implementation of the RWAMP persisted until present time, and has successfully led to maintenance of wolf breeding pairs and pup recruitment (Gese *et al*., unpublished).

Notwithstanding these efforts, red wolf recovery in North Carolina has been fraught with challenges, including human-caused mortality (USFWS 2007; Sparkman *et al*. 2011). Some mortality is from shooting, either intentionally via wolf poaching or else from mistaken identity during legal coyote hunting (USFWS 2007). Wolves also die of unknown causes or go missing, which may reflect "cryptic poaching" by individuals seeking to destroy evidence of illegal wolf mortality (Smith *et al*. 2010; Liberg *et al*. 2012). In 2014, in an attempt to reduce wolf mortality, conservation groups launched a legal challenge against the State of North Carolina with the intent of closing coyote hunting in the recovery area, to improve survival of wolves and placeholder coyotes/hybrids (Red Wolf Coalition *et al*. v. Cogdell *et al*., No. 2:13-cv-60-BO [E.D. N.C. filed October 17, 2013]). The legal challenge ultimately resulted in a ruling banning coyote hunting in the recovery area (Red Wolf Coalition *et al*. v. Cogdell *et al*., No. 2:13-cv-60-BO, 2014 WL 1922234 [E.D. N.C. May 13, 2014]). However, shortly after this decision the State of North Carolina requested that USFWS review the red wolf recovery program, specifically to determine "feasibility of achieving a stable, self-sustaining red wolf population" and "the appropriateness of the experimental program" (G. Myers to C. Dohner, June 2, 2014). In response, the USFWS initiated an external review with a final decision on the program's future expected by early 2015 (*U.S. Fish and Wildlife Service Southeast Region News Release*, August 29, 2014).

The red wolf presents an interesting dilemma regarding endangered species recovery in a human-dominated landscape currently occupied by an interbreeding species subject to legal harvest. This situation raises thorny issues concerning human dimensions in wildlife management, endangered species recovery policy, and state-federal jurisdiction in conservation (see Scott *et al*. 2005, 2010; Redford *et al*. 2011). To help inform the ongoing program review and potential future direction of red wolf recovery, we compare demography of red wolves, coyotes, and hybrids in the North Carolina recovery area (1999–2007).

One metric of the RWAMP's success, and an indication of whether the red wolf population ultimately can become viable and self-sustaining (i.e., with no further need for intervention), is the predicted higher survival and/or productivity of wolves relative to coyotes/hybrids. Further, we assessed prevalence of causes of death among past (1999–2007) and current (2009–2014) canids to gauge whether gunshot mortality is substantive and increasing, and whether death from natural causes (i.e., strife) is an important mortality factor for coyotes/hybrids, as is predicted by the competitive exclusion hypothesis. Our results are presented in the context of red wolf recovery, and more generally, conservation policy for endangered species faced with substantive challenges to population recovery. However, recognizing that forces may seek to use this article to hastily support termination of the red wolf program, we urge that our findings be part of a larger analysis thoughtfully weighing ecological, social, economic, and political factors related to red wolf recovery.

Materials and methods

The red wolf recovery area constitutes the five easternmost counties in North Carolina, United States (Figure 1). Starting in 1987, red wolves were released on the Alligator River National Wildlife Refuge, and during 1987 to the present, free-ranging wolves were captured across the recovery area primarily via foothold traps, and equipped with very high frequency (VHF) radio-collars (Phillips *et al.* 2003). Radio-collared wolves were monitored every 3–4 days from the ground or via fixed wing aircraft, and dead animals were retrieved to assess cause of death. Death was attributed to anthropogenic, natural, or unknown causes, with anthropogenic mortality further distinguished as gunshot, legal take (damage control), illegal take (e.g., poison) or vehicle collision, and natural causes including intraspecific strife, disease, and malnutrition. Management-related deaths were censored, as were individuals who were missing due to lost signal. Coyotes/hybrids were subject to the same procedures starting in 1999, and our detailed analysis is restricted to the 1999–2007 period during which time demographic data were available from USFWS for different canid groups. We also extracted relevant cause of death information spanning 2008–2014 from published annual and quarterly reports (see http://www.fws.gov/redwolf/documents.html), to compare previous to current mortality patterns. We provide the minimum known wolf population, based on counts of radio-collared individuals (USFWS 2007) supplemented with counts reported in more recent annual and quarterly reports. While the majority of wolves and hybrids in the recovery area may have been radio-collared (and therefore known to observers), the abundance of coyotes was less clear.

Canids were assigned a taxonomic status through: (1) a genetic assignment test assessing allele frequency differences and presence of coyote-specific alleles (CSA) that are absent in red wolves but present in local coyotes (Miller *et al.* 2003), and (2) a genetically reconstructed pedigree (Stoskopf *et al.* 2005, Adams 2006). Based on criteria established by the RWAMP, animals with >87.5% red wolf ancestry were considered red wolves, those with 0 red wolf ancestry were coyotes, and those >0% and <87.5% were hybrids.

We described survival differences and annual survival rates between canid groups via the Kaplan–Meier (KM) estimator (Murray 2006). To provide robust hazard ratio estimates among canids, we used a Cox proportional hazards (CPH) model with genetic types as a dummy variable (red wolf being the reference category). To further examine red wolf parentage, we performed a second CPH analysis using dummy variables for age category, sex, and red wolf ancestry. Here, red wolf genetic contribution was represented using a continuous (%) variable. We used a right-censored design with time-at-risk based on time (days) since the animal's first capture (Fieberg & Delgiudice 2009), and evaluated main effects only. We tested whether average recruitment differed between wolves and hybrids by tallying counts of known pups per litter in fall (USFWS 2007) and using a Mann–Whitney–Wilcoxon test; coyotes were excluded in this analysis because sterilization effectively reduced coyote recruitment to zero. We report average recruitment values with 95% confidence intervals based on quantiles. The prevalence of wolf and coyote causes of death was compared using chi-square.

Results

Between 1999 and 2007, USFWS personnel monitored 218 red wolves, 36 coyotes, and 78 hybrids. Out of these, 144 animals died during the study and an additional 49 went missing. Annual survival rates (1999–2007) were comparable between groups (Table 1 & Figure 2); these results were corroborated by hazard ratios that were indistinguishable between coyotes (HR = 0.728, SE = 0.345, $P = 0.343$), hybrids (HR = 1.052, SE = 0.257, $P = 0.800$), and wolves (reference group, Figure 1). Further, a CPH model using percent red wolf ancestry failed to detect any influence of age class, sex, or percent red wolf ancestry on survival (Table 2). Red wolves and hybrids also did not differ in their rate of pup recruitment in fall ($W = 7319.5$, $P = 0.935$, Table 1).

Table 1 Annual survival rate (± 95 CI) and average number of pups recruited (± 95 CI) for 332 canids (red wolves, hybrids, coyotes) in eastern North Carolina (1999–2007)[a]

Group	*n* (Survival)	Annual survival	*n* (Recruitment)	Recruitment
Red wolf	218	0.794 (0.709, 0.889)	80	1.201 (0, 5)
Hybrid	78	0.798 (0.706, 0.902)	33	1.270 (0, 6)
Coyote	36	0.778 (0.662, 0.912)	0	–

[a]The analysis is restricted to animals whose genetic composition was known, and ranged from 0% to 100%

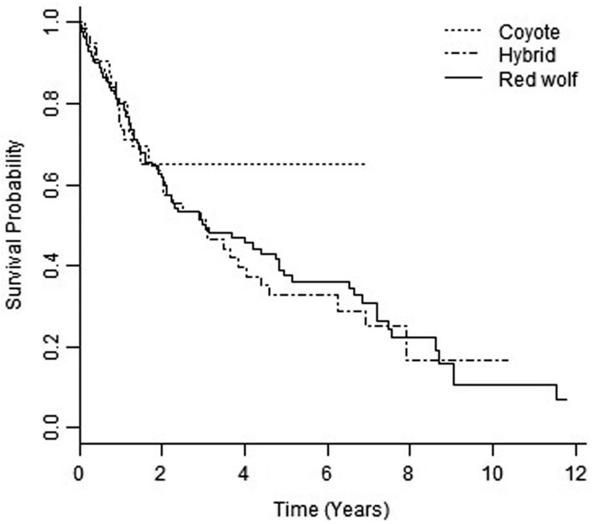

Figure 2 Kaplan–Meier survival estimates of 332 red wolves, coyotes, and hybrids, 1999–2007. The analysis is restricted to animals whose genetic composition was known, and ranged from 0% to 100%.

Causes of death from our primary analysis (1999–2007) differed from those prevailing more recently (2009 to March 2014) (wolves: $\chi^2{}_6 = 17.4$, $P = 0.008$; coyotes/hybrids: $\chi^2{}_3 = 11.3$, $P = 0.010$). Most canid mortality was from gunshot, which was consistently 6–7% more prevalent for wolves than coyotes/hybrids. A higher proportion of wolves succumbed to unknown mortality, whereas a higher proportion of coyotes/hybrids went missing, meaning that it is unclear whether unspecified wolf mortality is due to cryptic poaching. For wolves, illegal take increased, whereas natural mortality decreased, through time. For coyotes/hybrids, prevalence of vehicle collisions and missing individuals increased, whereas deaths from unknown or other causes decreased. Importantly, natural mortalities were generally rare and declined to zero among coyotes/hybrids (Figure 3), meaning that wolves did not kill coyotes.

The number of known wolves in the recovery area reached a plateau in the early 2000s and remained largely consistent or declined slightly since then (Figure 4). Between 1999 and 2013, number of known adult wolves varied between 62 and 103 individuals, whereas number of known wolves (including pups) ranged from 97 to 128 individuals. Earlier, carrying capacity of known wolves (including pups and adults) was estimated at 139 individuals, and total wolf numbers in the area could be 40–60% higher than known wolf counts (USFWS 2007).

Table 2 Cox proportional hazards model for of 332 red wolves, coyotes, and hybrids monitored for survival in eastern North Carolina (1999–2007)[a]

Variables	Hazard
Pup	0.997 (0.439, 2.261)
Yearling	0.945 (0.556, 1.604)
Male	0.945 (0.672, 1.327)
% red wolf ancestry	1.003 (0.996, 1.009)

[a]Hazard ratios (+/− 95% CI) are presented. Pup and yearling values are relative to the risk for adults. The analysis is restricted to animals whose genetic composition was known, with values ranging from 0% to 100%.

Discussion

We found comparable survival and recruitment rates and variable causes of death among canids, and stationary or declining wolf numbers through time. Gunshot mortality removed both wolves and sterilized placeholder coyotes/hybrids, was consistently more prevalent in wolves, but was not more prevalent through time. Natural mortality was less common and declined to zero for coyotes/hybrids. Accordingly, while the RWAMP is successful insofar as providing red wolves with conditions allowing them to survive and produce young, such conditions likely are insufficient to give wolves the demographic advantage that will promote establishment of a self-sustaining population in the absence of intervention. One important aim of the recovery program is to reach a stage where wolves saturate the landscape and naturally exclude coyotes/hybrids through competition and strife (Murray & Waits 2007). Despite that numerical requirements for red wolf recovery are more modest than for most other endangered species (220 free-ranging individuals, see USFWS 1990; see also Neel *et al.* 2012), and that considerable financial, personnel, and logistical investments are made each year in the RWAMP (see USFWS 2009–2013; Gese *et al.*, unpublished), basic conditions conducive to wolf population self-sufficiency simply have not been achieved.

Red wolf recovery experienced a variety of setbacks since its inception in 1987 (Phillips *et al.* 2003; Stoskopf *et al.* 2005), with wolf shooting and coyote hunting being longstanding concerns. Yet, the ongoing program review should be considered as an opportunity to chart a new direction in red wolf conservation, one that reflects the realities of contemporary landscapes, complex

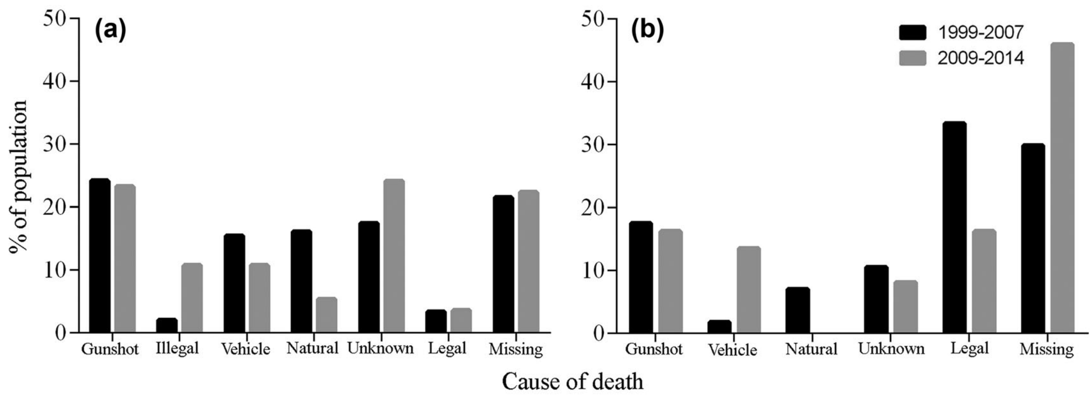

Figure 3 Fates of red wolves (a) and non-wolf canids (b, including coyotes and hybrids) in eastern North Carolina. We compare previous (1999–2007) to current (2009–2014) fates; current fates were obtained from annual or quarterly reports (http://www.fws.gov/redwolf/documents.html). The fates are: gunshot, illegal take (e.g., poison), vehicle collisions, natural mortality (strife, senescence, disease), legal take (wildlife damage control, coyote/hybrids only), unknown causes, and missing from the study.

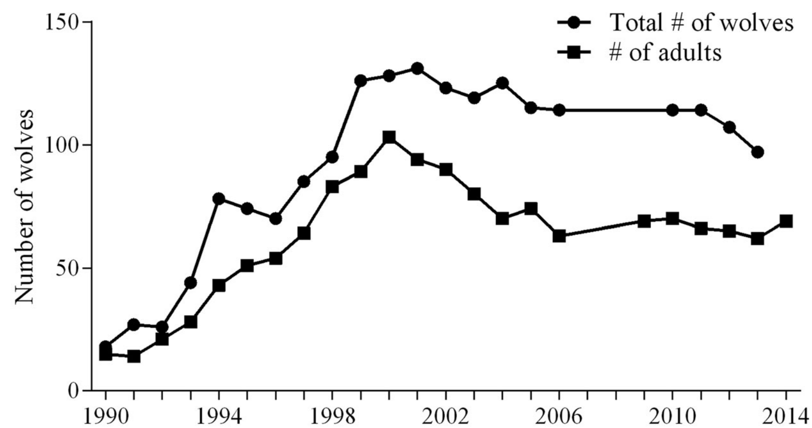

Figure 4 Number of known red wolves in eastern North Carolina (1990–2013). Counts are based on USFWS records (1990–2006; USFWS 2007) or on fall (adult) or spring (pup) counts provided in quarterly reports (2009–2013; http://www.fws.gov/redwolf/documents.html).

human dimensions, and changing standards and expectations regarding endangered species recovery. Central to the issue of coyote hunting is whether gunshot mortality is compensatory (i.e., replaces other mortality and does not increase total mortality), additive (i.e., does not replace other mortality but increases total mortality), or superadditive (i.e., does not replace other mortality but increases total mortality beyond that caused by the mortality source; Murray *et al.* 2010). For example, if shooting deaths among adult wolves lead to pup starvation, pack breakdown and subsequent dispersal of remaining members, or increased hybridization with coyotes/hybrids, gunshot mortality may be superadditive. Sparkman *et al.* (2011) sought to address this question but results were equivocal and our more detailed survival analysis was constrained because contemporary data (2008–2014) were not available. Additional analysis of the 1999–2007 data does not reveal a higher mortality risk among breeding wolves relative to nonbreeders (D. Murray, unpublished), although including contemporary data in this analysis would be especially helpful. However, it stands to reason that at least some shot wolves otherwise would have survived and contributed demographically to population growth, meaning that gunshot mortality must be at least partially additive (see Murray *et al.* 2010; Bohling & Waits, unpublished). In addition, shooting sterilized coyotes/hybrids undoubtedly compromises the role of such animals as placeholders, as part of the RWAMP. Therefore, if all coyotes/hybrids in the recovery area can be sterilized and removed opportunistically as per the RWAMP, the recent ban on coyote hunting in the recovery area should provide a net benefit for wolf recovery.

Yet, even if permanent threat abatement (i.e., banning coyote hunting) is fully successful, it is unclear whether improved wolf survival and recruitment will provide sufficient demographic advantage to override perpetual colonization of the recovery area by coyotes/hybrids. Wolf demographic rates reported here are on par with those observed in stationary or increasing wolf populations elsewhere (Fuller *et al.* 2003), meaning that there is limited room for demographic improvement. Coyotes now occupy virtually the entire eastern coast of North America (Stoskopf *et al*. 2005; Murray & Waits 2007), meaning that the threat of hybridization with recovering red wolves is strong and pervasive. That unlike most wolf populations, red wolf territories in North Carolina are not contiguous and vacant landscape persists in the interstitial spaces (USFWS 2007; Gese *et al*., unpublished), speaks to marginal wolf habitat in the recovery area and the constant opportunity for colonization by coyotes/hybrids; these animals may have lesser territorial requirements and more plastic habitat needs than wolves. Not surprisingly, habitat loss is a pervasive impediment to species recovery in contemporary North American landscapes (Kerr & Deguise 2004; Schwartz 2008). Accordingly, it may simply not be possible to achieve competitive exclusion of coyotes/hybrids by red wolves in North Carolina (see Murray & Waits 2007). Thus, despite significant and commendable efforts through the RWAMP, we do not fully agree with calls for more research on fundamental questions to help improve red wolf recovery success in the present recovery area (see Hinton *et al*. 2013; see also Way 2014). Alternatively, such investigations may prove valuable if they are placed in the broader context of wolf colonization in the northeastern United States, or endangered species recovery under threat of hybridization and human persecution.

Conservation applications

Our results provide an important lesson regarding implementation of endangered species recovery in contemporary landscapes and under demanding social conditions. For red wolves, it seems appropriate to embrace the ongoing program review as an opportunity to refine recovery goals. Recent philosophical shifts in conservation biology prompted important dialogue redefining endangered species recovery in light of achievable goals that: (1) are ecologically sufficient, standardized, and defensible (Flather *et al.* 2011; Neel *et al*. 2012; Hutchings & Kuparinen 2014; Westwood *et al*. 2014), (2) favor recovering landscapes and ecosystems rather than single species (Tear *et al*. 1995; but see Clark & Harvey 2002; Male & Bean 2005; Bottrill *et al*. 2011), and (3) reflect that some contemporary landscapes are colonized most appropriately by replacement species serving as surrogates for parental species (see Platt & Connell 2003; Wiens *et al*. 2008). The red wolf may be an ideal candidate for such reevaluation, and options worthy of examination might include considering the species as recovered under revised recovery goals that accept establishment and maintenance of a small population requiring perpetual intervention (as per protocols established in the RWAMP), establishment of a new, more suitable recovery area where long-term intervention is not required (if such an area is available), or acceptance that whichever canid eventually colonizes the recovery area in the absence of intervention will be best adapted to a contemporary North Carolina landscape. In our opinion, such deep philosophical discussions will be evidence of a maturing discipline of conservation biology, one that is grounded in reality and pragmatism, and one that reflects exceedingly challenging ecological, social, economic, and political conditions associated with endangered species recovery in present times. However, we caution that the current timeline and level of rigor afforded the ongoing red wolf program review is unlikely to achieve such expectations.

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