ECOLOGICAL EFFECTS OF A DECLINING RED WOLF POPULATION

By
ALEXA MURRAY

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Approved by advisory committee:
Lara Pacifici, chair
Roland Kays, co-chair
Ron Sutherland, co-chair
Krishna Pacifici, co-chair

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Abstract

Carnivores, especially wolves (*Canis* sp.), have profound impacts on their ecosystems, affecting the abundance and behavior of prey and competitors, but this has not been examined for red wolves (*C. rufus*). We studied a population of red wolves that was reintroduced to eastern North Carolina in 1987, initially thrived, but experienced a population crash in 2014. We evaluated changes in the relative abundance of prey and competitor species during the red wolf decline with 25 camera traps run in the Red Wolf Recovery Area from 2015 – 2021. If red wolves were having an ecological effect on the mammal community, we expected this effect would decline as the wolf population waned, resulting in increases in prey and competitor populations. Supporting this, we found that relative abundance increased for most prey and competitor species including American black bear (*Ursus americanus*), bobcat (*Lynx rufus*), Virginia opossum (*Didelphis virginiana*), and Northern raccoon (*Procyon lotor*). For all species this increase was most notable after spring 2018, the first season without wolf reproduction. For some species, the increase was dramatic, with a doubling of the detection rate for raccoon, bear, and bobcat in the spring of 2021 compared to the spring of 2018. Our results support the hypothesis that red wolves had a strong effect on their ecosystems by suppressing prey and competitor populations when they were at their peak. The delay between the wolf decline and ecosystem response suggests that there could be a 2–3-year time lag in the effects of the wolf population on the species around them and/or that the ecological release was only notable when the wolves reached their lowest population size and failed to breed. This study shows that reintroduction of large predators can play important ecological roles, but their effects decline if their numbers dwindle to critically low numbers.

Keywords: red wolf, endangered species, North Carolina, relative abundance, camera traps
Introduction

Populations of the world’s large predators are declining globally due to conflict with humans (Di Marco et al. 2014). Many of the world’s largest carnivore species are listed as vulnerable, endangered, or critically endangered, with over 75% of their populations currently declining (Ripple et al. 2014) and losing large parts of their historic ranges (Prugh et al. 2009). As these large predators were disappearing from the landscape in the last fifty years, researchers realized that these carnivores play vital ecological roles. Ensuing research showed that predators can have top-down effects on the behavior and populations of other species, controlling prey populations, limiting competitors, and stabilizing food webs (McLaren & Peterson 1994, Estes et al. 2011). As researchers began to recognize the importance of these ecosystem services, predators were protected, and have even been reintroduced into regions where they were previously extirpated.

One of the most well-known predator restoration programs is the reintroduction of gray wolves (Canis lupus) to the Greater Yellowstone Ecosystem (GYE) from 1994—96 by the US Fish & Wildlife Service (USFWS). When wolves reappeared on the landscape, they had cascading effects on the ecosystem. The reintroduced gray wolves preyed primarily on elk (Cervus canadensis), reducing herd sizes, and providing food for scavengers like brown bears (Ursus arctos) (Smith, Peterson, & Houston 2003, Ripple & Beschta 2012, Ordiz et al. 2020). Smaller elk herds on the landscape resulted in less intense grazing, leading to increases in aspen (Populus tremuloides) and cottonwood (Populus sp.) (Ripple & Beschta 2012, Ripple, Beschta, & Painter 2015). Wolves also outcompeted coyotes (Canis latrans) and drove them out of their territories, benefitting smaller predators and rodents that were preyed upon by coyotes (Miller et al. 2012). Some biologists have even speculated that the presence of wolves has led to changes in the soil microbes and river pathways in the GYE (Frank 2008, Beschta & Ripple 2019). Although there are researchers that have contested some of the results of these trophic cascade studies (Fleming 2019, Brice 2022), the Yellowstone wolf reintroduction remains one of the most striking experiments demonstrating the effects large predators can have on an ecosystem, and thus the value of protecting and restoring predator populations.

The Yellowstone wolf reintroduction was modelled off an earlier reintroduction of red wolves (C. rufus) into North Carolina. Red wolves were once found throughout the east coast of the United States but their numbers declined in the 1800’s and early 1900’s due to intense predator control and habitat loss (Manganiello 2009, Hinton, Chamberlain, & Rabon 2013). Government biologists began capturing the last wild wolves in Texas and Louisiana in the 1970s to start a captive breeding program and eventually, in 1980, declared the red wolf extinct in the wild. Starting in 1987, USFWS released wolves into Alligator River National Wildlife Refuge in eastern North Carolina. Within six years, the population had over 50 individuals and was rising steadily, their numbers bolstered by new releases of animals from the captive breeding program every year as well as natural breeding of the wolves in the wild. Red wolves hit a peak of around 120 individuals in 2006 and remained around this level until 2012, when the population began to decline due to conflict with some local residents resulting in high rates of illegal hunting (Hinton et al. 2017b). The USFWS halted reintroductions of animals from the captive breeding program in 2009, and the wild red wolf population dropped to a maximum of just 17 animals in
2021. Further, there was no natural breeding in the wild population from 2010-2021. After many political delays surrounding the release of new wolves into the population, the Red Wolf Recovery Area released 10 captive individuals again in winter 2022. (Red Wolf Recovery Program, 2022).

While certain aspects of the behavior and ecology of the reintroduced red wolf population has been well-studied (Sparkman et al. 2011, Dellinger et al. 2013), the only research into the ecological impact of the wolves has focused on diet comparisons with coyotes (C. latrans). Coyotes are slightly smaller than red wolves and feed on similar prey species, leading some researchers to conclude that red wolves will outcompete coyotes due to the limited niche partitioning available (McVey et al. 2013, Hinton et al. 2017a). Given their diet, (McVey et al., 2013) we expect that red wolves would have the strongest impact on prey species including white-tailed deer (Odocoileus virginianus), lagomorphs (Sylvilagus sp.), raccoons (Procyon lotor), and small rodents. Aside from coyotes, we also predict that red wolves would have a negative effect on populations of similar sized predators including bobcats (Lynx rufus) as well as the larger and omnivorous American black bears (Ursus americanus). Past research has shown that gray wolves suppress coyotes, which then benefits smaller canids (Smith et al. 2003). However, given the smaller size of red wolves, and the lack of larger ungulate species in this ecosystem, we predict that red wolves might also suppress populations of red fox (Vulpes vulpes) and gray fox (Urocyon cinereoargenteus).

Here we evaluate the influence of red wolves on the mammal community by using camera traps to determine trends in the relative abundances of prey and competitor species during the period when the reintroduced population of wolves was declining (2015-2021). If the once healthy red wolf population was having an effect on the ecosystem, we hypothesize that the relative abundance of sympatric species would increase when the wolves declined. Our results are relevant not only for this endangered species, but for any reintroduction program interested in using predators to restore balance to an ecosystem.

Study Area

Our study takes place in the Red Wolf Recovery Area that consists of five counties in eastern North Carolina: Tyrell, Dare, Washington, Beaufort, and Hyde. The original wolves were introduced into Alligator River National Wildlife Refuge (ARNWR) in Dare County, but the recovery area was expanded as the population grew too large to stay inside the refuge and began dispersing into the surrounding areas. Our cameras are mostly consolidated within ARNWR and Pocosin Lakes National Wildlife Refuge (PLNWR), with a few outside of those areas (Fig. 1).
Figure 1: Our red wolf study took place in eastern North Carolina, primarily within the Alligator River and Pocosin Lakes National Wildlife Refuges. The inset shows our 25 camera locations.

Methods

We used camera traps placed on trees approximately 0.5 meters (knee-height) off the ground and aimed at nearby roads or trails. Cameras were placed at least two kilometers apart from each other to ensure independent detections. Cameras were set to take three photos at every trigger and there was no delay interval. We used Reconyx and Moultrie camera traps with a fast (0.5 seconds) trigger time. We used an independence interval between detections of one minute to group consecutive images into sequences, and then calculated detection rate for a species as the number of sequences per day. For the first year of the study, the data were entered and processed in eMammal (McShea et al. 2016). Starting with data from the summer of 2016, we switched to Wildlife Insights for storing and cataloguing images (Ahumada et al. 2020). A number of students and interns helped identify wildlife pictures, but all Canis species were identified by RK or RS as red wolves, coyotes, or “unknown canids” based on size and body proportions.

We used data from cameras run at 25 locations (Figure 1) from June 2015-November 2021 to conduct these analyses, giving us a total of 7,453 trap nights. Cameras failed intermittently due to a variety of reasons (battery failure, memory card filled up, destruction by bears, theft, hurricanes, etc.) so we chose to combine data into 3-month periods representing “quarters” and structured around biological seasons (Figure 2): Spring ran from March-May and included red wolf pupping season, Summer was June-August and included deer fawning season, Fall was September-November and included deer mating season, and Winter was December-February and included red wolf mating season. We only used camera locations with at least 14 days of sampling per quarter, resulting in a time series of 27 quarters from 2015-2021.
We used detection rate of a species by camera traps as a measure of relative abundance, which has been shown to be correlated with density in a number of species (Heilbrun et al. 2006, Parsons et al. 2017). Detection rates can be affected by a variety of factors other than abundance (Hofmeester et al. 2019), but because we standardized field protocol over time, we suggest that it is a useful measure for comparing relative abundance over time. After downloading the data from eMammal and Wildlife Insights, we used program R (R Core Team, 2021) to calculate the detection rates of target species at each camera in each quarter by dividing the number of independent detections by the number of days that camera was operational during that quarter. To prevent cameras with overall higher detection rates from having outsized effects on trends over time we calculated z-scores from detection rates for each species across all cameras. Because some species showed strong seasonal trends, and our interest was in longer-term changes, we calculated a moving average (two quarters before, one after) of the z-scores to remove this seasonal effect from the trend lines. This process is demonstrated using the American black bear data in Figure 3.
A) Detection Rates

B) Z-scores

C) Average Z-score

D) Moving Average of Z-scores
We obtained yearly population estimates of red wolves in the recovery program from the US Fish & Wildlife Service webpage (Red Wolf Recovery Program, 2022). Biologists with USFWS monitor these wolves via GPS collars that are tracked daily, and the census information is released to the public annually in July via the webpage. The annual census includes an estimate of how many wolves remain in the recovery area, births, deaths, captive releases, and cross-fostered puppies. Any new adult wolves released into the recovery area are fitted with GPS collars, and puppies are monitored carefully, receiving their own GPS collars after their first winter, so population estimates are assumed to be quite accurate.

Because the wolves were originally released inside ARNWR, where they are best protected from poaching, there have always been wolves inside the refuge and the decline in wolf population was more dramatic outside the refuge boundaries (until 2018, when the population declined in the refuge as well). Thus, we would expect that any effects from the wolves on other species would be strongest outside the refuge, and for some analyses we spatially divided the cameras into those inside/outside the refuge.

**Results**

We obtained a total of 46,950 independent detections of wildlife: 1,193 of birds and 45,757 of mammals (Table 1). Some species caught on camera over the course of this study, such as vultures, butterflies, and even turtles, were relatively rare and not part of our target group of animals (i.e. prey and competitor species of red wolves), thus they were removed from analyses. Of the species remaining in our analyses, American black bear and white-tailed deer had ten and six times, respectively, as many independent detection events as any other species or species group. Lagomorphs were relatively rare and can be hard to tell apart on camera, so we grouped those two species (*Sylvilagus floridanus* and *S. palustris*) together. Similarly, red wolves and coyotes are also difficult to distinguish on camera, with 37% of *Canis* detections classified as “unknown canids” (Supplementary Figure 1). Because of the uncertainty, we were unable to include any *Canis* species in our analyses of population trends. Instead, we relied on the USFWS estimates of wolf populations, which showed a sharp decline from 2014 to 2016 and a plateau at a low of around twenty individuals since then (Figure 4).
We obtained a total of 27 quarterly estimates of relative abundance for six of the most common potential prey species and four likely competitor species. Four of the species showed strong seasonal variation in detection rates (Supplementary Figures 2A-L) including bears being most active in the summer and least active in the winter, and bobcats showing the opposite pattern. Turkeys were detected more often in the spring and deer were seen more often in the fall.
We found consistent increases in relative abundance for most large and medium-sized species throughout the study, but most notably after spring 2018 (Figure 5). In particular, raccoons, opossums, bears, and bobcats have increasing trends after that quarter. Turkeys show an overall increase in relative abundance from the start of the study through fall 2021. Deer also hit a low point in spring of 2018 and trended upward afterwards, as seen in other species. However, deer had a unique sharp decline in the winter/spring of 2020 followed by another increase. Smaller prey species, such as lagomorphs and gray squirrels didn’t show any obvious trends over the time period. Red foxes, although generally rare, were the only species to show a (slightly) decreasing trend in relative abundance over time, while gray foxes showed no obvious trend.

Figure 4: US Fish & Wildlife Service red wolf population estimates 1987-2022 in the Red Wolf Recovery Area (data from USFWS).

Red bars indicate years in which there was no red wolf reproduction in the wild.
Figure 5: Moving averages of z-scores for our 10 target species from winter 2015-summer 2021, split between those considered prey species and those considered potential competitors. Our results show a general trend of increasing relative abundance for most of these species during our study.

Given the consistent change in the trend of relative abundance of species starting in spring 2018, we compared detection rates of target species between spring 2018 and spring 2021 as an indication of the overall magnitude of change in abundance over time (Figure 6). Bears, opossums, bobcats, and raccoons showed a significant increase in detection rates between spring 2018 and spring 2021. All of these species increased by at least 128%, with opossums increasing by a huge margin of 314%. Deer, turkeys, and squirrels, while not significant, still showed an increase of at least 9% in detection rates over time.

![Figure 6: Average detection rates for seven species in the spring of 2018 vs the spring of 2021. A * indicates non-overlapping standard error bars (black lines).](image)

Splitting the cameras into inside/outside the refuge resulted in reduced sample size and led to high variance, preventing the evaluation of population trends per quarter, but we do present three time points that had better sample sizes to compare broad trends (Supplementary Figure 3). While the large confidence intervals limit firm conclusions, the population increases tended to be larger outside the refuge, where wolf populations were lower. Increasing trends were still notable for most species inside the refuge, excepting deer, which were relatively stable.
Discussion

We present the first analysis of the ecological effects of red wolves on prey and competitors, using the dramatic recent decline of wolves as a natural experiment. We found substantial increases in both prey and competitor abundances following the decline of red wolves, supporting the hypothesis that the recently larger red wolf population had considerable ecological impacts. The change in population trajectory was synchronized with most species starting an upward trend in 2018, which we suggest could reflect the result of a time lag effect in combination with the wolf population falling below a threshold number of breeding wolves to have an effect. Alternatively, the trend may simply be a reflection of the local decline of red wolves at Alligator River National Wildlife Refuge happening later than the decline experienced by the broader wolf population.

Overall, we found that most species increased in relative abundance over the course of our study, including four of six prey and two of four competitors. We found that white-tailed deer and raccoons, two well-known prey species of red wolves (McVey et al. 2013), showed a general increase. The increase in raccoons after the decline of the wolves is an example of the mesopredator release hypothesis (Crooks & Soulé 1999) and supports the idea that coyotes don’t limit raccoon populations like wolves do (Gehrt & Prange 2007). Overabundance of raccoons can cause problems with diseases such as rabies and raccoon roundworm (Baylisascaris procyonis) that are problematic for both humans and other species (LoGiudice 2006, Beltrán-Beck, Garcia, & Gortazar 2012), so having a predator that can regulate their population size is important for healthy ecosystems. Squirrels and lagomorphs seemed generally unaffected by the decline of the wolves. These smaller prey species can typically sustain predation pressures and are less affected by one predator because of their life history characteristics and fast reproductive cycles (Reznick, Bryant, & Bashey 2002). Opossums and turkeys were not important food items in previous studies of red wolf diets (McVey et al. 2013), so it’s unclear if the increase in those populations is the result of changes in red wolf foraging. Turkeys especially may still be recovering from earlier population collapses.

Given the importance of white-tailed deer in the diet of red wolves, we were expecting them to respond the strongest to wolf decline. While the relative abundance of deer did increase after winter 2018, the pattern was messier than for other species, with a subsequent decline in winter/spring 2020 that is not explained by the wolf population. It is not immediately obvious what could have caused that unexpected dip—hunter harvest was not unusual in those years (White-tailed Deer Harvest Reports, 2023.), no local disease outbreaks were noted (Boggess, M., personal communication), and precipitation and temperature were typical for the region (Weather averages Manteo, North Carolina, 2023). It is possible that any relationships between wolves and deer in this region might be obscured by effects of the abundant bear population. Black bears are common predators of fawns (Kautz et al. 2019) and were the most commonly detected species in the study site (Table 1), which is unusual. For example, in the 45 sites monitored with camera traps in eastern deciduous forests by the Snapshot USA project in 2019, only Dare County, NC (which includes ARNWR) had more detections of bears than deer (Cove et al. 2021). We suspect the large (and growing) bear population, combined with the lower quality of the pocosin swamp habitat for deer, contribute to the relatively low abundance of deer compared with
other parts of the state (e.g. as seen with state-wide occupancy models by Pease, Pacifici, & Kays 2022). Nonetheless, deer were still the second most common mammal detected by our cameras, and thus are still quite abundant even in the presence of these two large predators.

Our results showed that two out of the four potential competitor species also increased during this study with bobcats and black bears both increasing significantly from spring 2018 to spring 2021. A study conducted in Washington showed that bobcats coexist with coyotes, but tend to shift their temporal patterns to avoid gray wolves (Shores et al. 2019). Our results suggest that red wolves can have similar competitive effects on bobcats. There is some evidence of interference competition between gray wolves and black bears in places where they overlap (Ballard, Carbyn, & Smith 2003), but because red wolves are smaller, we expected there would be little direct competition between the two. Thus, we were surprised to see such a strong increase in their abundance, particularly after the wolves hit their population low of around 20 individuals. We suspect that a growing deer population is supplementing an already healthy population of bears, which also rely heavily on the planted crops within the refuge (Ditmer et al. 2016). Both refuges within the recovery areas (Alligator River and Pocosin Lakes) are protected from bear hunting, leaving the bear populations completely intact. Both red and grey foxes did not appear to show any obvious overall trends in relative abundance over the course of this study, although both were relatively rarely detected. Many studies have shown that foxes compete more directly with coyotes than they do with wolves (Harrison, Bissonette, & Sherburne 1989, Smith et al. 2003, Levi & Wilmers 2012), so it’s not surprising that we did not see a response to the wolf population decline.

The dramatic two-year crash of the red wolf population from 2014-2016 gives us the unique opportunity to consider how long it takes a species to respond to changes in their trophic cascades. Given the strong seasonal breeding of these populations, increases from reproduction or immigration would take at least one year to bolster population numbers. However, our results show a marked increase in most prey and competitor species relative abundances two to three years after the wolf decline, suggesting that there could be a time lag effect. This also corresponds to a time when the wolf population was at its lowest and there was no natural wolf reproduction occurring. Thus, reduced hunting by wolves not having a litter to provision for could have further limited the ecological impact of these wolves. We expect that a combination of a demographic time lag effect and a lack of wolf breeding explain the 2–3-year delay in prey and competitor species’ responses to the wolf decline.

Alternatively, the effect of wolves on other species could be very location-specific, as wolves inside the refuge declined later than the overall wolf population. We were able to look at spatial differences between detection rates for those inside ARNWR and those outside of the refuge. We didn’t find anything significant in those analyses, but it was a good reminder that the overall trends that we found might not be indicative of trends at finer spatial scales. A constant wolf presence inside ARNWR as well as the unique geography of the peninsula may have more of an effect on other species, like deer, that seemed to decrease over time within the refuge but increase overall. The increases in relative abundance for almost all species was more pronounced at camera locations outside of ARNWR where wolf populations fluctuated more and even dropped to 0 animals in 2017 and 2018 (Madison, J., personal communication). The idea that local trends in wolf abundance are driving more of these
relationships in abundances is a plausible one, but our sampling design did not allow for robust spatial analyses.

Thanks to our long-term monitoring efforts, we were able to see some interesting seasonal trends in a few species. Bears were more active in the summer and less active in the winter months, which coincides with hibernation (Hamilton & Marchinton, 1980, Hellgren & Vaughan, 1987). Interestingly, bobcats showed the opposite pattern—more activity in the winter months—which agrees with the findings from Chamberlain, Leopold, and Conner (2003) who thought that bobcat movement might be greatly effected by human use of study sites. Deer were detected more often in the fall, during rutting season (Lincoln, 1992), while turkeys were moving around more in the spring, most likely because of their breeding biology, as well (Carey, Lohr, & Kays, 2022).

Our study provides the first evidence of the ecological effects of red wolves by taking advantage of a long-term dataset but has some limitations. First, we don’t have a control site without wolves monitored throughout the same period, and so we can’t isolate the effects of declining wolves from other factors that might have been changing over this period. Nonetheless, there were no obvious large-scale changes in land management, habitat, or climate during this period that could have affected wildlife in a consistently positive way. Additionally, we recognize that camera trap detection rate is not the best measure of animal abundance, but this was the only option for analyzing these data, since individuals could not be identified uniquely to estimate density. Furthermore, by standardizing our methods and comparing z-scores over time, we minimize the most risky factors of using detection rate as relative abundance (Sollmann et al. 2013). However, the one factor we could not isolate is activity level—overall increases in the amount animals move could elevate detection rate without any changes in population size (Rowcliffe et al. 2014). We acknowledge this could be a concern when comparing across seasons but suggest this is an unlikely explanation for long-term changes in detection rates across multiple years. It is also important to note that because the camera traps were not deployed until 2015, we can only report on community-level changes following the red wolf decline. We cannot comment on the effects of an increasing or large red wolf population. Another study is currently comparing the camera detection rates for canids and mesopredators to ground-nesting northern bobwhite quail (Colinus virginianus) to determine if the wolves potentially have a positive effect on quail through mesopredator suppression. Future studies could also improve this kind of work by collecting additional data to estimate densities of entire mammal communities (Rowcliffe et al. 2008) and by using BACI designs that include control sites (Miller, Kays, & Leung 2020).

The decline of the red wolf population, while tragic, has given us an opportunity to observe their effect on the ecological community around them. We saw that a decline in the red wolf population was followed by increases in the population of many of their prey and competitors. The decline of the apex predator in this ecosystem obviously has consequences. Our results suggest that healthy populations of red wolves play important roles in regulating mesopredator and herbivore populations, which could help control disease and prevent overexploitation of a habitat. Other reintroduction efforts have had success at establishing large predator populations and they have seen those ecosystems thrive. Thus, our results support continuation and expansion of the Red Wolf Recovery Program, showing that the presence of these large predators in an area can help restore ecosystem balance.
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References


Boggess, M. NC Wildlife Resources Commission, personal communication.


Supplementary Figures

Supplementary Figure 1: Number of detection events for coyotes, red wolves, and unknown canids listed here as “Canis species.” Due to the difficulty in distinguishing between red wolves and coyotes in camera trap pictures, there is a large category of unknowns, and thus, much uncertainty surrounding the relative abundances of any canids measured in this study.

Supplementary Figure 2A: Detection rates, z-scores, and seasonality over time for coyotes.
Supplementary Figure 2B: Detection rates, z-scores, and seasonality over time for red wolves.

Supplementary Figure 2C: Detection rates, z-scores, and seasonality over time for opossums.
Supplementary Figure 2D: Detection rates, z-scores, and seasonality over time for bobcats.

Supplementary Figure 2E: Detection rates, z-scores, and seasonality over time for turkeys.
Supplementary Figure 2F: Detection rates, z-scores, and seasonality over time for white-tailed deer.

Supplementary Figure 2G: Detection rates, z-scores, and seasonality over time for raccoons.
Supplementary Figure 2H: Detection rates, z-scores, and seasonality over time for Eastern gray squirrels.

Supplementary Figure 2I: Detection rates, z-scores, and seasonality over time for gray foxes.
Supplementary Figure 2J: Detection rates, z-scores, and seasonality over time of American black bears.

Supplementary Figure 2K: Detection rates, z-scores, and seasonality over time for red foxes.
Supplementary Figure 2L: Detection rates, z-scores, and seasonality over time for lagomorphs (Sylvilagus sp.).

Supplementary Figure 3: Average detection rates for seven species in Spring 2016, Spring 2018, and Spring 2021. The top panel shows the detection rates inside Alligator River National Wildlife Refuge and the bottom panel shows the detection rates outside of the refuge. The horizontal black bars indicate standard error. A) shows the detection rates for only black bears and white-tailed deer, as they were significantly higher than the other species (B).