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Ecological effects of a declining red wolf population

A. Murray[1], R. Sutherland[2] & R. Kays[1,3]

1 Department of Forestry and Environmental Resources, NC State University, North Carolina Museum of Natural Sciences, Raleigh, NC, USA

2 Wildlands Network, Durham, NC, USA

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

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Correspondence

Alexa Murray, Department of Forestry and Environmental Resources, NC State University, Raleigh, NC, USA.

Email: alexa.murray1928@gmail.com

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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 in detail for red wolves (*C. rufus*). We studied a population of red wolves that was reintroduced to eastern North Carolina in 1987 and initially thrived, peaking at 120 animals. Due to an increase in anthropogenic mortality and a decline in government support, the population experienced a crash starting in 2014. We evaluated changes in the relative abundance of prey and competitor species during the red wolf decline with 25 camera traps run primarily on National Wildlife Refuges from 2015 to 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 increased 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 second year with low red wolf reproduction. For some species, the increase was dramatic; the detection rate for raccoon, bear and bobcat doubled from the spring of 2018 to the spring of 2021. White-tailed deer (*Odocoileus virginianus*) showed a general increase in relative abundance but remained prevalent even at their lowest detection rates. Our results lend correlational support to the hypothesis that red wolves had a strong effect on their ecosystems by suppressing prey and competitor populations when they were at their peak. This study adds to the growing body of evidence that reintroductions of large predators have ecological impacts, with the caveat that these impacts can decline rapidly if the predators dwindle back to critically low numbers.

Introduction

Populations of the world's large predators are declining globally due in large part to conflict with humans (Di Marco *et al.*, 2014). Many predator 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). After what has been, in some cases, centuries of human persecution of top predators, in recent decades researchers realized that they play vital ecological roles (Estes, 1996; Ripple *et al.*, 2014). Ensuing investigations showed that these 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 and the public began to better recognize the importance of these ecosystem services, predators were protected in some areas and have even been reintroduced into regions where they were previously extirpated (Hayward & Somers, 2009; Ripple & Beschta, 2012).

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 to 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 modeled 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 1800s and early 1900s due to intense predator control and habitat loss (Manganiello, 2009; Hinton, Chamberlain, & Rabon, 2013). Government biologists began capturing the last wild red 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 red wolves into Alligator River National Wildlife Refuge in eastern North Carolina. Within 6 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 red 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 rapidly due to conflict with some local residents resulting in high rates of illegal hunting (Hinton *et al*., 2017b). For political reasons, the USFWS halted releases of red wolves from captivity in 2014 and stopped the coyote management (sterilizations and stricter coyote hunting regulations) that had been employed to try to limit hybridization between red wolves and coyotes (Hinton *et al*., 2017b; Red Wolf Recovery Program, 2022). Furthermore, in 2017 and 2018, only four pups were born in the wild each year, and then from 2019 to 2021 there was no natural breeding in the wild population. As a result of these factors, the wild red wolf population dropped to an estimated 17–20 total animals by 2021, with at times only eight radio-collared and confirmed adult red wolves remaining in North Carolina. However, a court order in 2021 forced USFWS to begin releasing red wolves again, and by May 2023 the wild population is expected to reach over 30 animals (Red Wolf Recovery Program, 2022).

While certain aspects of the behavior and ecology of the reintroduced red wolf population have been well-studied (Sparkman *et al*., 2011; Dellinger *et al*., 2013), the only research into the ecological impact of the red wolves has focused on diet comparisons with coyotes (*C. latrans*). Coyotes are about half the size of 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*) with uncertain competitive impacts on the much larger (and omnivorous) American black bears (*Ursus americanus*). Past research has shown that gray wolves suppress coyotes, which then benefits smaller canids such as foxes (Smith, Peterson, & Houston, 2003). However, given the smaller size of red wolves, and the lack of larger ungulate prey species in this ecosystem, we predict that red wolves might also suppress populations of red fox (*Vulpes vulpes*) and gray fox (*Urocyon cinereoargenteus*) through direct competition for prey.

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 red wolves was declining (2015–2021). If the once healthy red wolf population had an effect on these species, we hypothesize that the relative abundance of sympatric species would increase when the red wolves declined. Our results are relevant not only for this endangered species but also for any reintroduction program interested in restoring predators.

Study area

Our study takes place in the Red Wolf Non-Essential Experimental Population Area that consists of five counties in eastern North Carolina: Beaufort, Dare, Hyde, Tyrell and Washington. The original red wolves were introduced into Alligator River National Wildlife Refuge (ARNWR) in Dare County, but the non-essential experimental population designation under the Endangered Species Act expanded the area to the other four counties to accommodate the growing population. Our cameras were mostly consolidated within ARNWR and Pocosin Lakes National Wildlife Refuge (PLNWR), with a few outside of those areas (Fig. 1).

Materials and methods

We used camera traps placed on trees approximately 0.5 m (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, at least for most prey species such as deer. 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 s) trigger time. We used an independence interval of 1 min between detections to group consecutive images into sequences, which has been shown to remove most temporal autocorrelation (Kays & Parsons, 2014). We 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 cataloging images (Ahumada *et al*., 2020). A number of students and interns helped

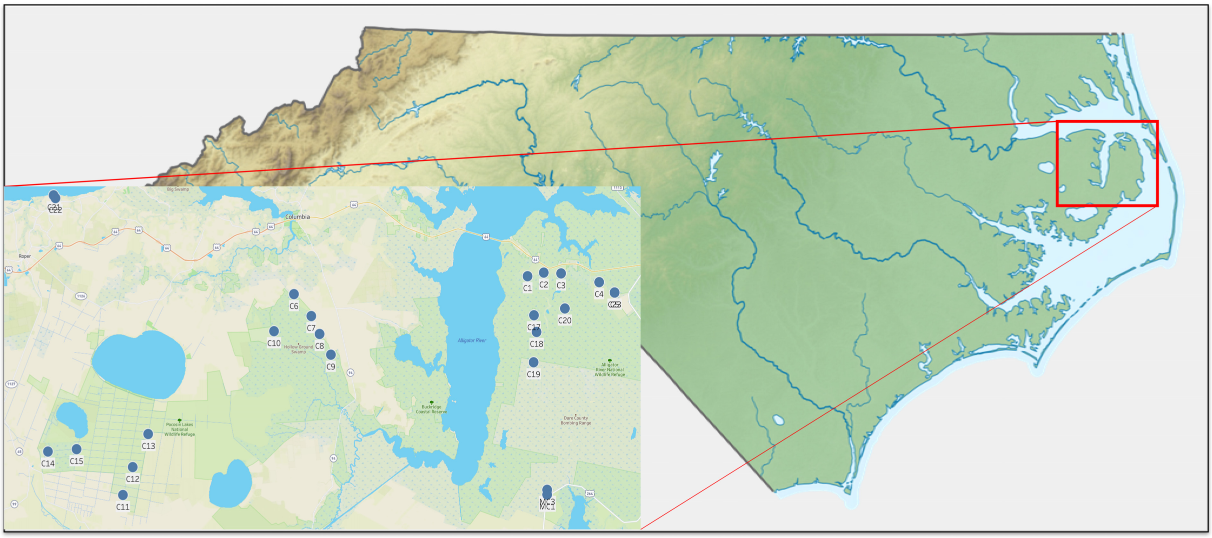

Figure 1 Our red wolf study took place in eastern North Carolina, primarily within the Alligator River and Pocosin Lakes National Wildlife Refuges. The inset shows our 25 camera locations.

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 (Fig. 1) from June 2015–November 2021 to conduct these analyses, giving us a total of 7453 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 (Fig. 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 to 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 Fig. 3.

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/VHF collars and update the estimated population size on their website as it changes. The annual census includes an estimate of how many wolves remain in the population area, births, deaths, captive releases and fostered puppies. Any new adult wolves released 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 Alligator River refuge and the decline in wolf population was more dramatic outside the refuge boundaries (until 2018, when the population declined inside the refuge as well). Thus, we would expect that any effects from the wolves on other species would be strongest outside ARNWR, and for some analyses we spatially divided the cameras into those inside/outside that refuge.

Results

We obtained a total of 46 950 independent detections of wildlife: 1193 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 10 and

Figure 2 Timeline with vertical bars showing when camera traps were active at 25 locations in the Red Wolf Recovery Area from summer 2015 to fall 2021. Relative abundance estimates were calculated for each quarter (colors) with at least 14 days of data.

6 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' (Figure S1). 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 red wolf populations, which showed a sharp decline from 2014 to 2016 and a plateau at a low of around 20 individuals since then (Fig. 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 (Figure S2A–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 (Fig. 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 afterward, 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 did not 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.

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 (Fig. 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.

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 (Figure S3). While the large confidence intervals limit firm conclusions, the population increases tended to be larger outside of Alligator River National Wildlife Refuge, in areas where wolf populations were lower (Figure S4). Increasing trends were still notable for most species inside the refuge, except deer, which were relatively stable.

Discussion

We present the first analysis of the potential ecological effects of red wolves on prey and competitors, using the dramatic recent decline of the wolves as a natural experiment. We found substantial increases in both prey and competitor abundances following the decline of red wolves, potentially 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

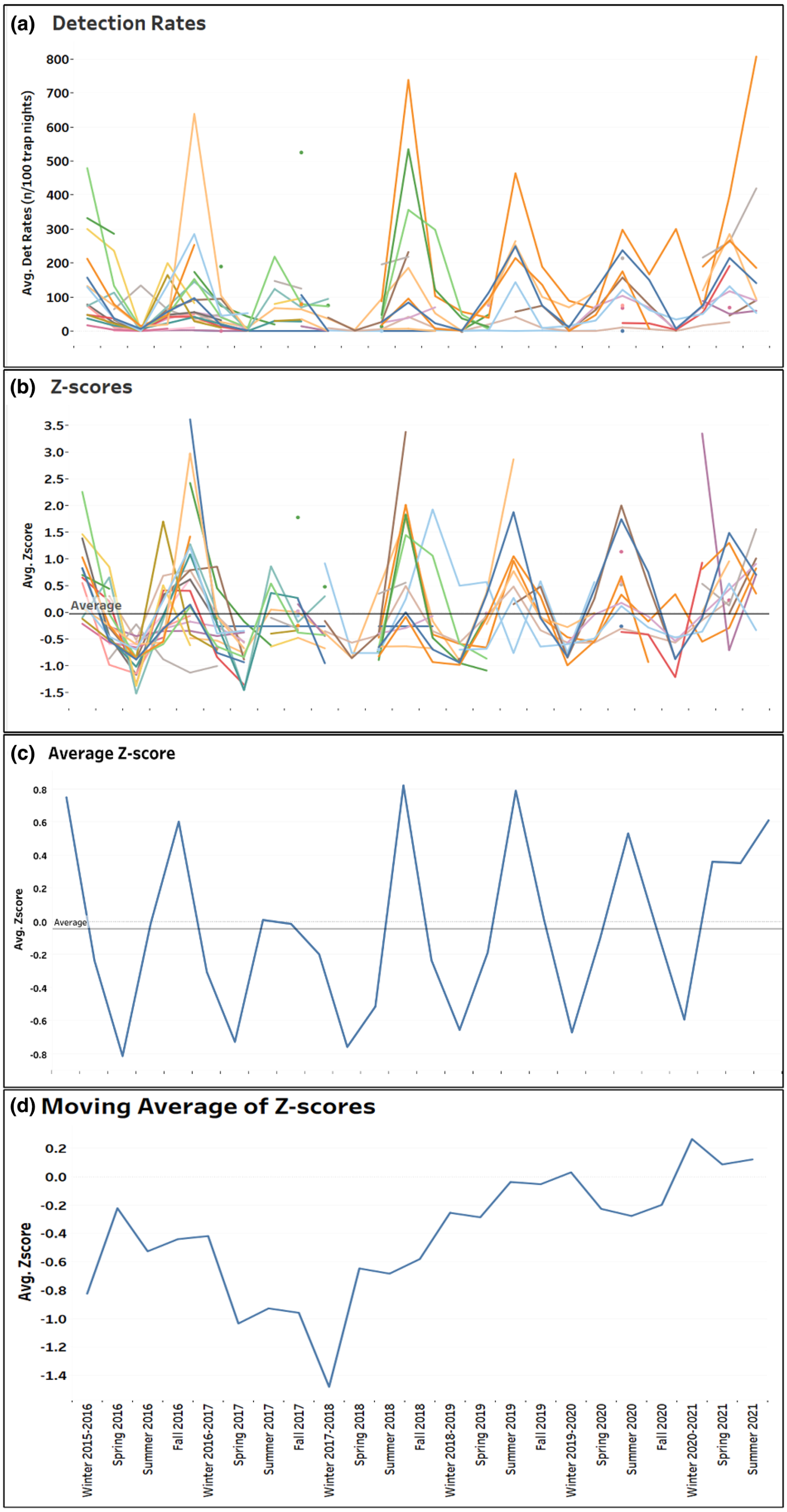

Figure 3 Demonstration of how we obtained our abundance trend lines using American black bears as an example. (a) We calculated detection rates for each camera location (colored lines) per quarter, discarding those deployments with fewer than 14 trap nights. (b) We then determined the *z*-scores for each location and (c) averaged across all the camera locations. In this case, a strong seasonal effect is seen where bears are most common in summer and rare in winter. (d) Finally, we took a moving average of the *z*-scores to remove seasonality and obtain a general trendline for each species. For bears, we see a steady increase in relative abundance after winter 2017/2018.

wolf population falling below a threshold number of breeding wolves to have an effect. Alternatively, or conjunctly, the trend may reflect that the local decline of red wolves at Alligator River National Wildlife Refuge happened later than the decline experienced by the broader wolf population. It is important to keep in mind the limitations of this correlational study that, while long in comparison with many camera trapping efforts, still only covered a 7-year period. Other factors besides red wolves certainly may have been involved in the patterns we observed, and it is regrettable that no similar data are available for the time period when the red wolf population was expanding in size (1987–2012). However, we believe that the results have implications for predator reintroductions and small populations of large carnivores.

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 do not 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, García, & Gortázar, 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 is unclear if the increase in those populations is the result of changes in red wolf foraging. In particular, wild turkeys were apparently reintroduced to Pocosin Lakes National Wildlife Refuge in the early 2000's and the population has grown substantially since then (Stanton, n.d.).

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 more variable 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, n.d.), 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 among camera trap projects but not unexpected given the extreme density of bears in this part of North Carolina. 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

Table 1 number of independent detection events per species

Species	Number of independent detection events
Ursus americanus	20 554
Odocoileus virginianus	12 373
Lynx rufus	2515
Didelphis virginiana	2180
Procyon lotor	2129
Canis species	1468
Canis latrans	1380
Meleagris gallopavo	1193
Sciurus carolinensis	1161
Canis rufus	1076
Vulpes vulpes	332
Urocyon cinereoargenteus	310
Sylvilagus species	279

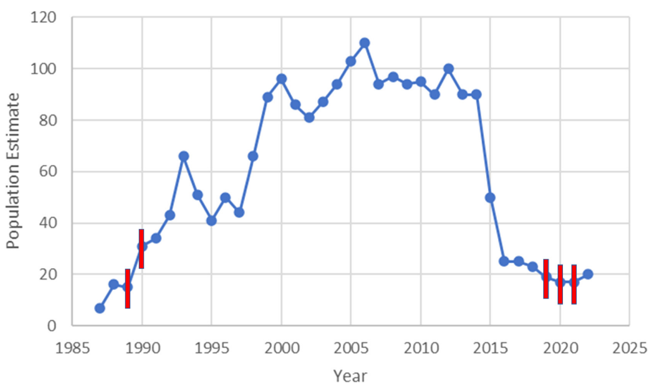

Figure 4 US Fish & Wildlife Service red wolf population estimates 1987–2022 in the Red Wolf Recovery Area (data from USFWS). Red bars indicate years in which there was no red wolf reproduction in the wild.

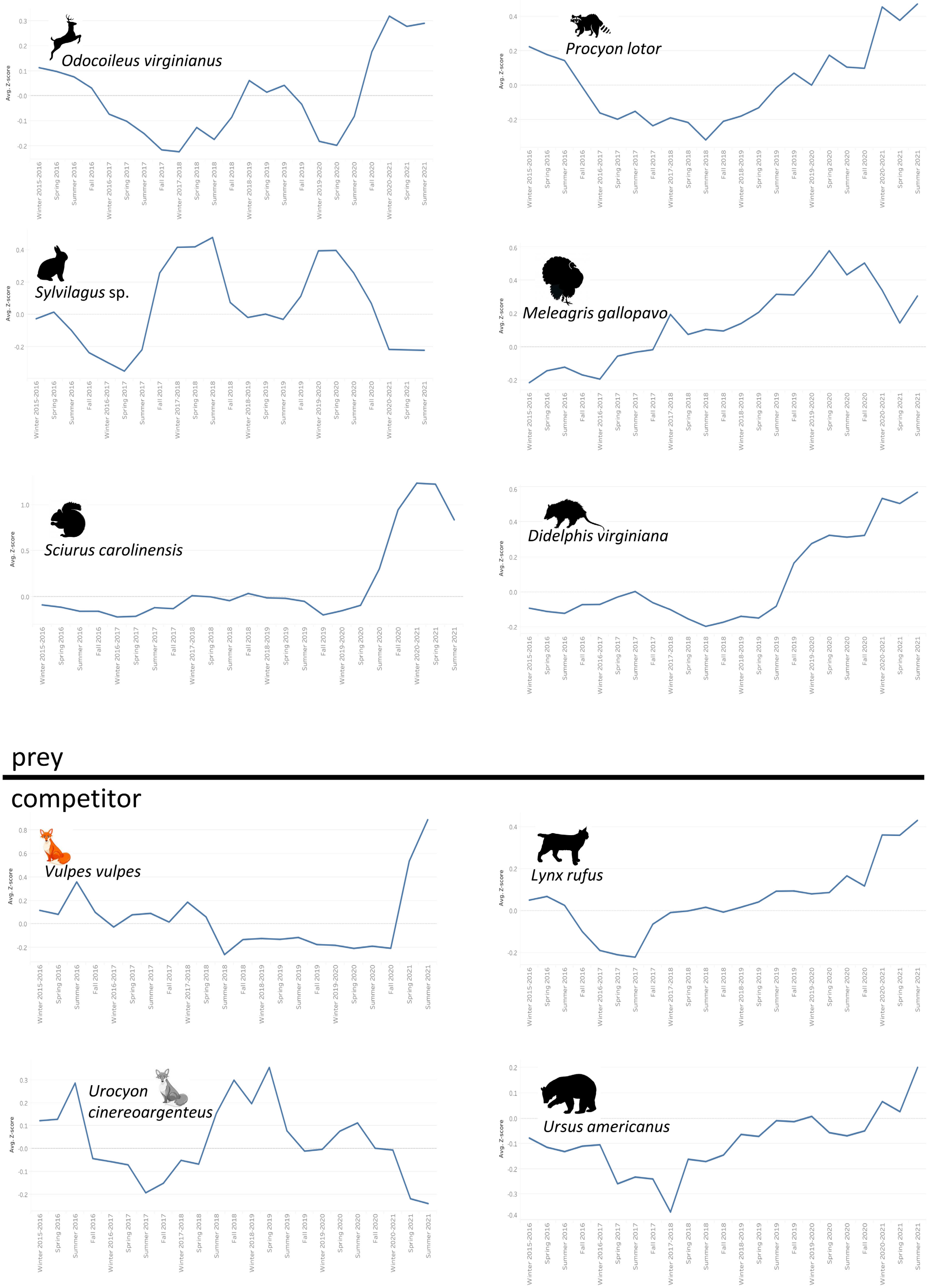
Odocoileus virginianus
Procyon lotor
Sylvilagus sp.
Meleagris gallopavo
Sciurus carolinensis
Didelphis virginiana
prey
competitor
Vulpes vulpes
Lynx rufus
Urocyon cinereoargenteus
Ursus americanus
Avg. Z-score

Figure 5 Moving averages of *z*-scores for our 10 target species from winter 2015 to 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.

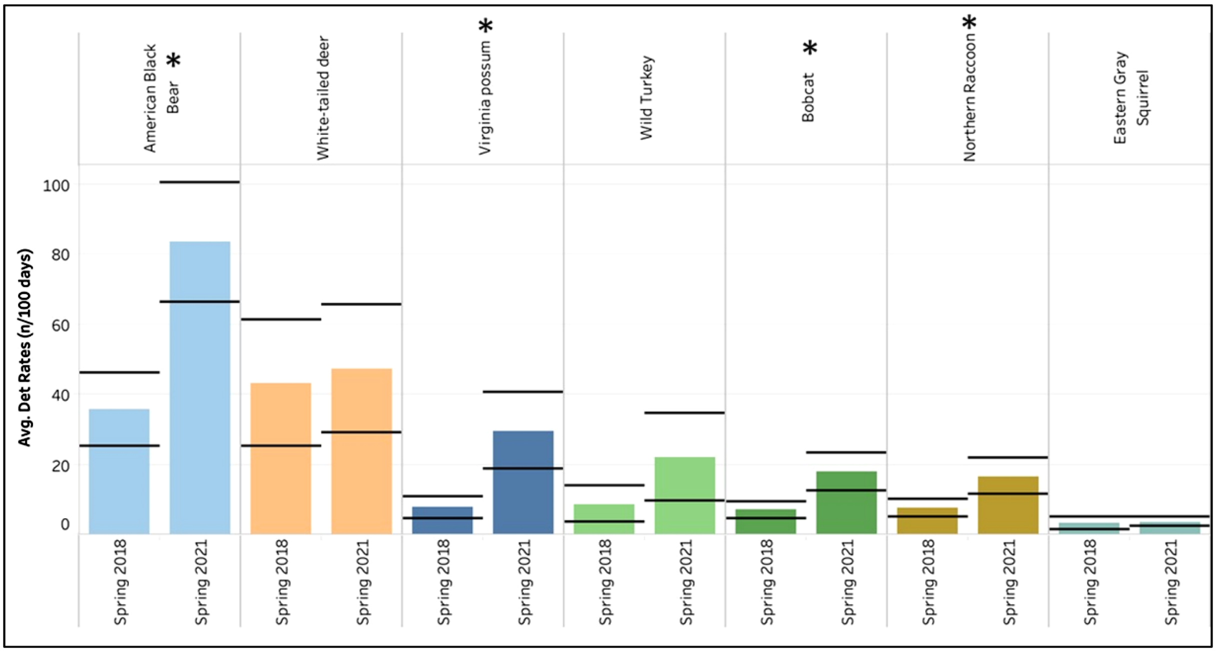

Figure 6 Average detection rates for seven species in the spring of 2018 vs the spring of 2021. A * indicates non-overlapping standard error bars (black lines).

(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, not to mention hunting by humans (both Alligator River and Pocosin Lakes National Wildlife Refuges are open to public deer hunting).

Our results showed that two out of the four potential competitor species also increased during this study with bobcats and black bears both increasing notably 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 may also have competitive effects on bobcats, which would not be surprising given the extent to which both species rely on rodent and lagomorph prey. 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 non-essential experimental red wolf population area (Alligator River and Pocosin Lakes) are protected from bear hunting, leaving the bear populations completely intact. Both red and gray 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, Peterson, & Houston, 2003; Levi & Wilmers, 2012), so it is not surprising that we did not see a response to the wolf population decline.

The dramatic 2-year crash of the red wolf population from 2014 to 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 1 year to bolster population numbers. However, our results show a marked increase in most prey and competitor species relative abundances 2 to 3 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.

The effect of wolves on other species could also be very location-specific, as wolves inside ARNWR declined later, and less, than the overall wolf population. Our consideration of spatial differences of prey and competitor population trends inside ARNWR and those outside of the refuge found them to be similar (Figure S3). A constant wolf presence inside ARNWR as well as the unique and isolating geography of the Albemarle peninsula may have more of an effect on other species, like deer, that seemed to decrease over time within the Alligator River refuge but increase outside. The increases in relative abundance for almost all species was more pronounced at camera locations outside of ARNWR where wolf populations fluctuated more (Madison, n.d.). 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.

By taking advantage of a long-term dataset, our study provides the first evidence of the ecological effects of red wolves, but the research has some limitations. First, we do not have a control site without wolves monitored throughout the same period, and so we cannot 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). 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. We also recognize that our use of 25 camera traps is below the recommended 40 cameras to characterize an area (Kays *et al*., 2020). However, the fact that our cameras were run for over 7 years helps bolster the sample size. More cameras would have also helped better document the spatial variation in animal activity, but we still feel that we have a good representation, especially given the relatively small size of the study area. 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 habitats. 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 and emphasize the importance of long-term camera trap monitoring in the area. In spring 2023, five red wolf puppies were born, and several other family units were released. By the end of June 2023, the population was estimated at 32 animals, the most since 2015.

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Author contributions

Ron Sutherland conceived and designed this project and collected data with the help of field technicians. **Alexa Murray** analyzed and interpreted the data, with significant help from RK. **Alexa Murray** drafted the paper, while **Ron Sutherland** and **Roland Kays** supplied revision suggestions. All authors approved the final version.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

Sutherland, R., Murray, A., Kays, R., Stevanovski, A. 2011. Last updated April 2023. Wildlands Red Wolf Survey Project

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Supporting information

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

Figure S1. 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.

Figure S2. (A) Detection rates, *z*-scores, and seasonality over time for coyotes. (B) Detection rates, z-scores, and seasonality over time for red wolves. (C) Detection rates, *z*-scores, and seasonality over time for opossums. (D)

Detection rates, *z*-scores, and seasonality over time for bobcats. (E) Detection rates, *z*-scores, and seasonality over time for turkeys. (F) Detection rates, z-scores, and seasonality over time for white-tailed deer. (G) Detection rates, *z*-scores, and seasonality over time for raccoons. (H) Detection rates, *z*-scores, and seasonality over time for Eastern gray squirrels. (I) Detection rates, *z*-scores, and seasonality over time for gray foxes. (J) Detection rates, *z*-scores, and seasonality over time of American black bears. (K) Detection rates, *z*-scores, and seasonality over time for red foxes. (L) Detection rates, *z*-scores, and seasonality over time for lagomorphs (Sylvilgaus sp.).

Figure S3. 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).