Trophic cascades between wolves (*Canis lupus*), deer (*Odocoileus virginianus)*, and browse plants in Northern Wisconsin and Michigan

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ABSTRACT

Forest understory composition has been severely compromised by the increased browsing associated with the overabundance of the white- tailed deer (*Odocoileus virginianus*) in northern Wisconsin and Michigan. As well, both upland and riparian tree species have also been shown to reduced growth due to ungulate browse pressure. The return of the gray wolf (*Canis lupus*) to the region may institute a trophic cascade which benefits these browse plants by causing deer to exercise caution when in the presence of wolves and forage less. I tested this hypothesis by surveying the abundance of Bunchberry Dogwood (*Cornus canadensis*) in areas of high and low wolf use. I additionally compared the heights and browse damage of willows (*Salix spp*.) between these two areas. There was no difference in Bunchberry Dogwood abundance. This could be due to difficulty in recolonizing or a legacy effect of high deer populations in the recent past. Willow heights between wolf use areas did not differ but browse damage of willows was greater in low wolf use areas, suggesting that these trees are able to withstand herbivory by deer. Future research could examine if deer overabundance has impacted other forbs in the region similarly.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) have been present in the Upper Peninsula of Michigan and Northern Wisconsin since the last glacial retreat (Doepker, Beyer & Donovan 1994). Pre-European settlement, deer populations were estimated to be somewhere between 5 and10 per/mi^2 (Doepker, Beyer & Donovan 1994). However, in the 20th century, the white-tailed deer's main predator, the gray wolf (*Canis lupus*), was targeted by humans because they were seen as a threat (Boitani 2003). In 1915, U.S. congress even mandated the eradication of large predators (Ripple, Rooney & Beschta 2010). In addition to the loss of the gray wolf, increasing food resources from agriculture and development have expanded the deer well beyond their historic ranges (Rawinski 2008). Therefore, white-tailed deer have reached astronomical levels throughout the country (Doepker, Beyer & Donovan 1994).

Deer overabundance results in the over browsing of the forest understory. This browsing alters the understory by suppressing forb species and thwarting tree regeneration (Rawinski 2008). With high deer populations, browse tolerant plant species are favored and the forest understory becomes increasingly less diverse (Ripple, Rooney & Beschta 2010).

However, since listed as an endangered species in 1974, the gray wolf has been slowly recovering in Minnesota, Wisconsin, and Michigan (Hammill 2008). In 2005, the northern Wisconsin population was over 400 (Hammill 2008). This return of top predators as well as awareness of deer overabundance has caused deer numbers to lower substantially in the area, though they are still higher than they were historically. Even still, over browsing consequences have been known to persist up to two decades after herbivore numbers are reduced, known as the "legacy effect" (Nuttle, Yerger, Stoleson, & Ristau 2011).

Weigmann and Waller (2006) resurveyed plant communities from 1950 in the Upper Great Lakes region and determined which species benefited during deer overabundance and which ones suffered. These were termed "winners" and "losers." Bunchberry dogwood (*Cornus canadensis*) was one of 21 species found to be a loser (Weigmann & Waller 2006). Deer browsing has caused this understory forb to decrease in abundance in the region.

In addition to forbs, many tree species suffer because of reduced regeneration due to browsing. Eastern Hemlock (*Tsuga canadensis*) and Northern White Cedar (*Thuja occidentalis*) are upland tree species that struggle to regenerate with heavy browsing (Rooney & Waller 2003).

When the terminal bud of these saplings is browsed, a lateral bud takes its role and the tree grows horizontally rather than vertically. This is what causes the shorter tree saplings. However, this effect has not been studied in riparian species such as willows (*Salix spp*.) in the region.

Predator presence may be influencing browse plants via a trophic cascade. In the Gallatin Range of Montana, Ripple and Beschta (2004) found the reintroduction of wolves reduced willow browsing pressure by elk, resulting in increased height of the trees. Elk were not necessarily avoiding areas with wolves but rather exercised “risk-sensitive foraging behavior” to avoid predation and therefore browsed less (Ripple & Beschta 2004). The same is true of Yellowstone National Park where the reintroduction of wolves has caused much of the riparian vegetation to grow taller (Ripple & Beschta 2003). These are all signs that the return of a top predator can help reduce browsing pressure and provide forest recovery.

With the permanent establishment of wolf pack to UNDERC in 2006 (Michigan DNR), a trophic cascade may exist causing the white-tailed deer to be more cautious when foraging in areas with the predator present and therefore should browse less. To study this, I sampled bunchberry dogwood in upland sites and willow saplings in riparian zones in areas of high and low wolf use. I hypothesize that in areas where wolves frequent, deer browse on both plant species will be reduced, resulting in a greater abundance of bunchberry dogwood and taller willow saplings with fewer browsed twigs.

METHODS

Study Site

This study took place on the University of Notre Dame Environmental Research Center (UNDERC) located on the border of Northern Wisconsin and Michigan’s Upper Peninsula. The region is classified as a having a humid micro thermal climate. The surrounding mesic forests are a mix of coniferous and deciduous with common species including aspen, birch, sugar maple, white pine, and swamp conifers. Willows and speckled alder are also common along the many bodies of water found on the property.

Previous studies have defined areas within the property as high and low wolf use. When choosing the sampling areas, I was not aware of the high and low wolf use areas of property to limit bias in data collection. After data collection was finished, plots were then assigned to either high or low wolf use areas.

Bunchberry Dogwood Survey

Bunchberry dogwood was sampled using 24 meander surveys each 45 minutes in length. Thirteen of these were in low wolf use areas and 11 were in high wolf use areas. The starting point of each survey was a randomly generated GPS point from which I did not stray more than 200m from throughout the survey (Figure 1). All points were located at least 400m from one another. Every 3 minutes during the survey a 1m radius circular plot was sampled. I counted the number of flowering bunchberry dogwood within this plot. Total abundance at from each survey was then calculated.

Willow Survey

Willows were sampled using eight by eight meter^2 plots. Twenty willow stands were chosen throughout property (Figure 1). Ten of these were in high wolf use areas and ten in low wolf areas. At each site, the height of every willow within the plot was measured. Willows over 2.4 m were simply counted and not measured because they were above the maximum reach of a deer (Beals, Cottam & Vogl 1960). In addition, the total number of twigs and number of twigs browsed were counted for each willow. For each plot the average willow height and percentage of browsed twigs was then calculated.

Statistics

Data for bunchberry dogwood abundance and abundance of willows over 2.4 m were transformed by first adding 0.5 to the raw data and then taking the square root to adjust for counts and the presence of zeros. Non normal data sets were analyzed using Mann-Whiney U tests between high and low wolf use areas, these included bunchberry abundance, abundance of willows over 2.4 m, and percentage of browsed twigs on willows. A standard t-test between high and low wolf use areas was run for average willow height.

RESULTS

Nine of the 24 sites sampled for bunchberry dogwood had an abundance of less than 5. Six of these 9 were located in low wolf use areas. The mean abundance of bunchberry in areas of high wolf use was 52 versus 37 in areas of low wolf use (Figure 2), but overall there was no significant difference in the means between high and low wolf use areas (U= 70, d.f.= 1, p= 0.2537).

There was no difference in the heights of willows between high and low wolf use areas (t= 1.523, d.f. = 18, p=0.15, Figure 3). The abundance of willows over 2.4 m between high and low wolf use areas did not differ either (U= 66, d.f. = 1, p= 0.224). Twig browse percentages of willows from the two areas did differ (U= 6, d.f. = 1, p= 0.00088) with those located in high wolf use areas being lower (Figure 4).

DISCUSSION

My hypothesis that the abundance of bunchberry dogwood would differ in response to the presence of wolves was not supported by my data, however the frequency of extremely low abundances of bunchberry dogwood in low wolf use areas suggests this forb is being affected. In addition, willows were not taller in areas of high wolf use as I anticipated. Yet, the mean browse percentages found suggest that my hypothesis that willows would be browsed more heavily in low wolf use areas was correct.

There are several potential explanations for why I did not find a substantial difference between high and low wolf use areas in this study. Though Weigmann and Waller (2006) found that during deer overabundance in the region, bunchberry dogwood's range shrank and the species also experienced a decrease in both total frequency and mean frequency, the legacy effect suggests that changes resulting from ungulate herbivory will persist until stand replacement. (Nuttle et. al 2011). Essentially the forest understory at UNDERC could still be exhibiting the impact of over browsing even though much of this pressure has been reduced since 2006.

The re-establishment of bunchberry dogwood to areas of high wolf use may also be slowed by the rhizomatous nature and brief seed lifespan of the forb as well (Burger 1987). One study done in the Great Smokey Mountains National Park found that even after 8 years of deer exclusion, spring flora susceptible to browse still had not recovered (Webster, Jenkins & Rock 2005). Webster et. al (2005) even propose that these flowering species may have reached a point of such low viability during deer overabundance that regardless of current browse pressure, those species may not be able to recolonize on their own. In addition to greater deer management, human restoration of forbs may be necessary for complete recovery (Webster et. al 2005).

Willows at UNDERC seem to have be less affected by over browsing. My results reveal that willows are definitely being browsed at greater intensities in areas of low wolf use however this is not affecting their height. For willows exposed to elk browse in Yellowstone, this did result in a height increase in response to wolf reintroduction (Ripple 2004). This was attributed to the ungulate's "perceived risk of predation" not necessarily actual presence of a predator (Ripple 2004). It takes several years for prey to recognize increases in predator populations and alter behavior as a result (Ripple 2004). Therefore, it may take several years after these behavioral changes to occur before differences in willow height would be noticeable.

However with wolves established in the area since 2006, the difference between mean heights in response to wolf use at UNDERC would most likely already be recognizable. Another study on ungulate herbivory in Yellowstone National Park proposed other factors that may undermine the influence of wolf presence on willow height including the availability of escape routes from wolves and water stress on the willows (Singer, Mark & Cates 1994). These are elements I did not quantify that may equally affect willow heights.

On the other hand, my results may also imply that willows at UNDERC are able to withstand deer browsing fairly well. Willows are a fast growing species that can reach heights above a deer's reach in 2-5 years (Wolff 1978). The similar abundance of willows over 2.4 m found between areas of high and low wolf use support this theory. Regardless of predator presence, willows at UNDERC are successfully reaching heights above deer browse.

Future research could examine the condition of other herbaceous species and how long the legacy effect persists on the forest understory. Other riparian species could also be studied for differences in height between high and low wolf use areas. Additionally, the impact of other factors on browse intensity such as deer escape routes could be examined.

Regardless, outcomes for forest understory species don't look promising. Bunchberry dogwood and other herbaceous species likely have been permanently affected by the deer population explosion. An increase in wolf populations in the area will help lower browse pressure due to their cascading effects. Yet Wisconsin deer management population goals are still set higher than historic levels (Wisconsin DNR 1998). Additionally, a decrease in hunters and a legal wolf season may negate the benefits of this trophic cascade. For much of the Great Lakes Region the future of the forests is unknown.

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TABLES AND FIGURES

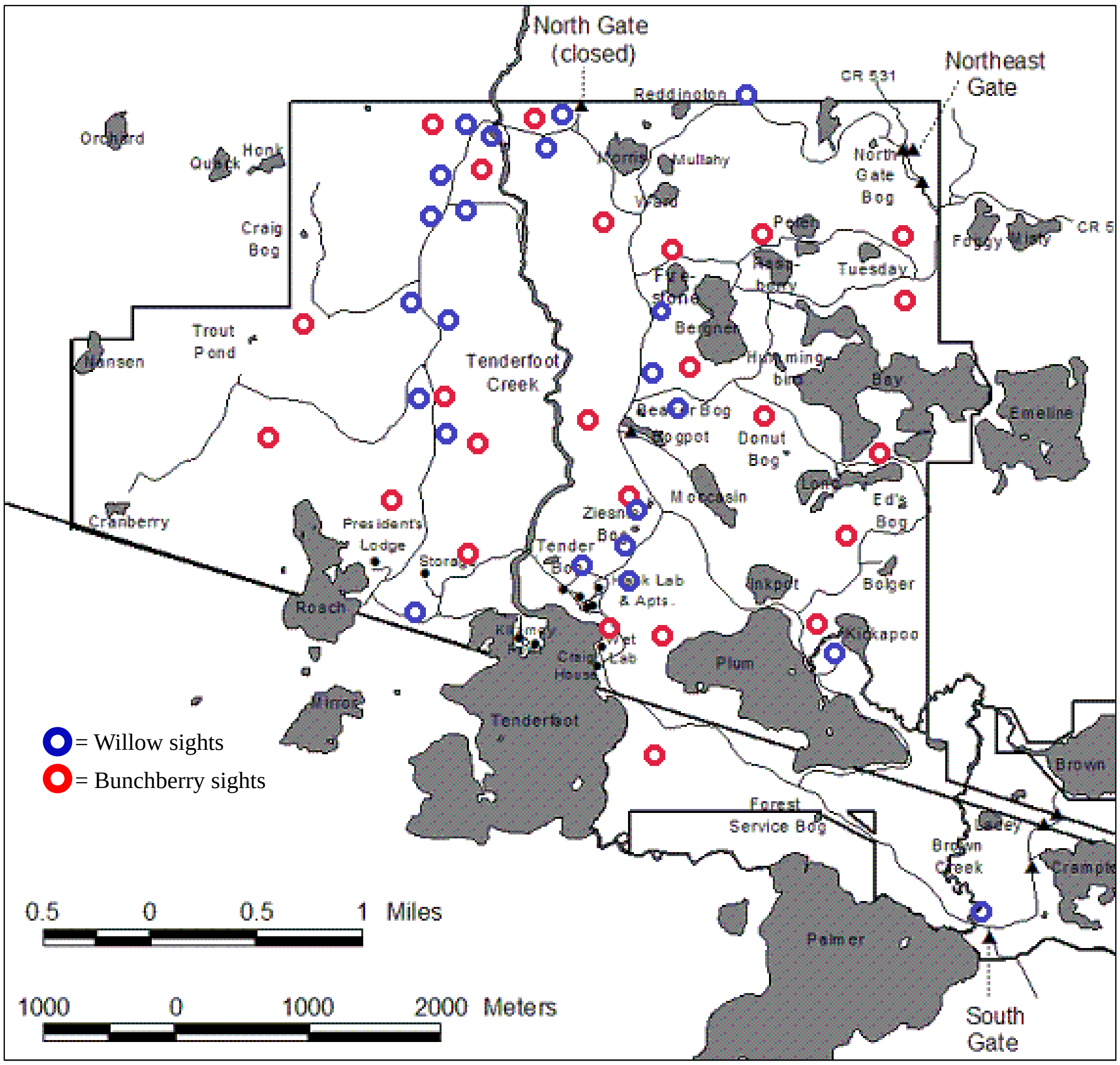

Figure 1. Sampling sights on the University of Notre Dame Environmental Research Center property

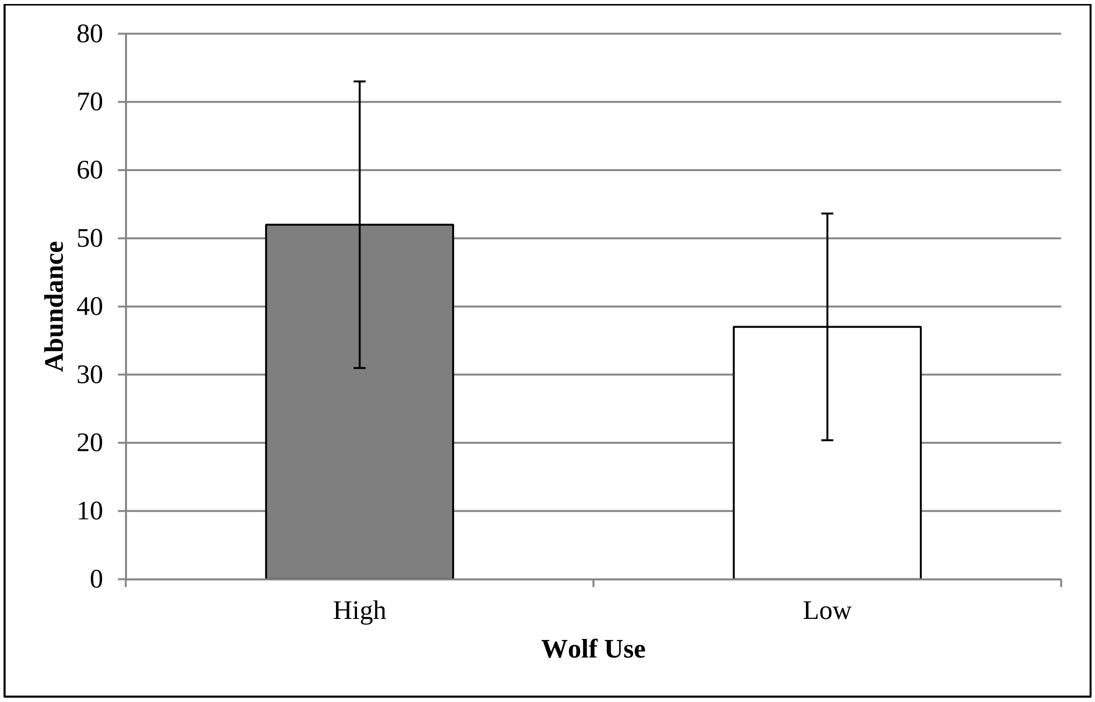

Figure 2. Mean abundance of bunchberry dogwood with standard error bars in areas of high and low wolf use at UNDERC.

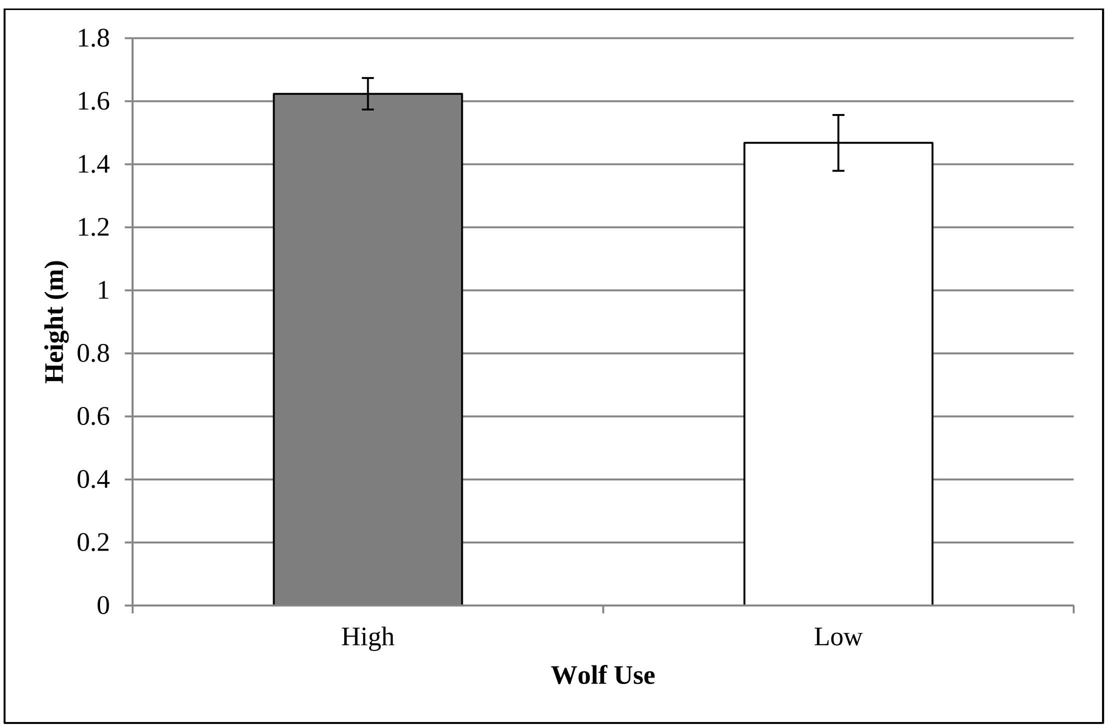

Figure 3. Mean height of willows with standard error bars in areas of high and low wolf use at UNDERC.

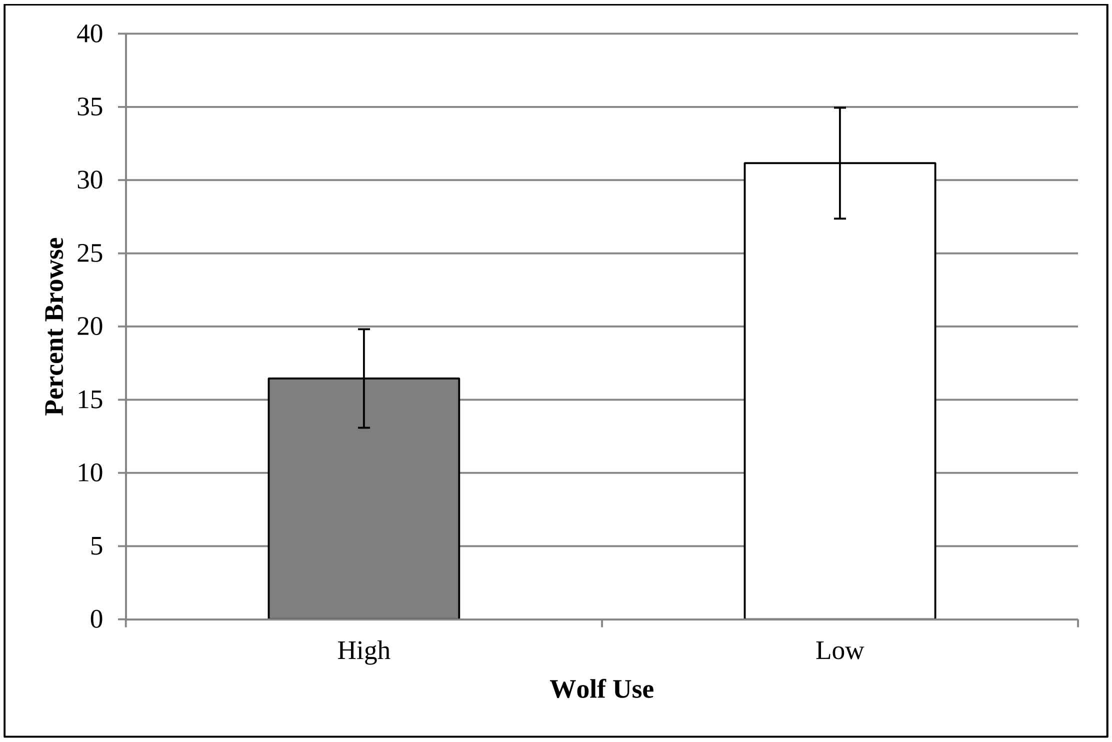

Figure 4. Mean percentage of browsed twigs on willows with standard error bars in areas of high and low wolf use at UNDERC