2015

Logging Debris Protects Sugar Maple (Acer Saccharum) Seedlings from White-Tailed Deer (Odocoileus Virginianus) Herbivory in Wolf-Occupied Forest

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LOGGING DEBRIS PROTECTS SUGAR MAPLE (*Acer saccharum*) SEEDLINGS FROM WHITE-TAILED DEER (*Odocoileus virginianus*) HERBIVORY IN WOLF-OCCUPIED FOREST

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science

By

Amy Erin Sullivan
B.S., Southeast Missouri State University, 2013

2015
Wright State University
I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY AMY E. SULLIVAN ENTITLED LOGGING DEBRIS PROTECTS SUGAR MAPLE (Acer saccharum) SEEDLINGS FROM WHITE-TAILED DEER (Odocoileus virginianus) HERBIVORY IN WOLF-OCCUPIED FOREST BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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ABSTRACT

Sullivan, Amy Erin. M.S. Department of Biological Sciences, Wright State University, 2015. Logging debris protects sugar maple (Acer saccharum) seedlings from white-tailed deer (Odocoileus virginianus) herbivory in wolf-occupied forest.

White-tailed deer are a species of great economic and ecological concern. Foresters sometimes leave logging debris known as slash on the forest floor with the intent to protect seedlings from deer herbivory and promote forest regeneration. I examined the effects of slash on rates of deer browsing on sugar maple seedlings in a forest of northern Wisconsin and measured deer foraging behavior using giving-up density and vigilance rates by employing trail cameras. Rates of browsed stems were almost twice as high in the open as within and adjacent to slash. These findings underscore the usefulness of slash for mitigating the effects of deer on tree seedlings. Deer vigilance did not vary by night and day but photos were rarely taken during dawn and dusk. These results may suggest that rather than using reactive vigilance behavior, deer are using proactive antipredator behavior and avoiding the study site at high-risk times.
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ACKNOWLEDGEMENTS

I thank my advisor Dr. Tom Rooney, as well as my other committee members, Dr. John O. Stireman III and Dr. Jeff Peters for their guidance. I also express my sincere gratitude to the other biology professors and the graduate students of Wright State University for their constant support. In particular, I am grateful to Holly Schlotman and Maureen McGeean for their assistance setting up the experiment.

I also take this opportunity to thank Dairymen’s, Inc and its members, especially Ralph Hewitt.
I. INTRODUCTION

Hyperabundance of cervids has become a major source of economic and ecological concerns worldwide. In the United States, white-tailed deer (*Odocoileus virginianus*) are the primary culprits in many areas, causing widespread ecological changes as well as economic damage and loss of life. One study estimated that over one million vehicle-deer collisions happen in the United States yearly. These accidents cause $1.1$ billion in repair costs as well as $29,000$ human injuries and over $200$ deaths (Conover et al. 1995). Agricultural damages by deer alone cost U.S. farmers over $100$ million annually, more than any other wildlife species (Conover 1997).

Deer populations have not always been high enough to reach these levels of destruction. U.S. densities of white-tailed deer have irrupted in response to a variety of human-caused factors, likely beginning with the widespread extermination of their primary predators (Ripple and Beschta 2005). Wolves, mountain lions, and bears in particular were subject to eradication efforts throughout much of the 1800s and early 1900s (Boitani 2003). Often, irruptions of deer populations followed (Ripple and Beschta 2005). These deer populations were often subsequently hunted to extremely low levels. In northwestern Pennsylvania, record low deer numbers occurred around 1900; shortly thereafter, the granting of legal protection for the animals, along with increased forage and lack of natural predators, allowed for a dramatic rebound to overpopulation levels (Redding 1995).
A similar pattern occurred in Wisconsin, with deer numbers increasing following predator extirpation, dropping due to human hunting, and quickly irrupting again following protection (Rooney and Waller 2003). White-tailed deer now live at densities around 10 individuals/km² in northern Wisconsin. Restricted hunting regulations, habitat fragmentation, and the loss of top predators are contributing factors (Rooney et al. 2002).

High-density deer populations such as these can have drastic impacts on the physical structure of forest understory as well as the composition, succession, and diversity of plant communities in general. In some systems, abundant white-tailed deer can drive herbaceous plant communities toward domination by less-palatable grasses and sedges (Rooney 2009). Browsing can also shift woody species composition (Bresette et al. 2012). In contrast, when deer are excluded, percent cover by broadleaf herbs and woody plants (Rooney 2009) as well as shrub and sapling density (Bresette et al. 2012) may be higher. In some cases, both density and diversity of woody understory plants can be improved by the exclusion of deer (McShea and Rappole 2000).

The impacts of deer herbivory are not limited to the understory. Browse on tree seedlings and saplings can impact regeneration of the forest itself. When cervids are densely populated, tree damage levels can be high, saplings stunted, and tree diversity decreased (Tilghman 1989, Angelstam 2000). The damage can lead to low recruitment of some trees, and may lead to a changed forest composition due to higher survival of browse-resistant species (Tremblay et al. 2007, Rooney and Waller 2003, Kittredge and
The potential for a reduction in desired species make cervid impacts on forests a major silvicultural concern.

Deer have also been linked to lower arthropod densities and biomass, which may be due in part to lower leaf litter accumulation in deer-heavy areas (Bresette et al. 2012). In cases where vegetative cover is reduced by deer browsing, soil moisture and humidity can be reduced while temperature and light levels increase (Rooney and Waller 2003), which can negatively impact gastropods as well (Suominen 1999). Vertebrate communities are susceptible as well. The decrease in cover caused by browsing may increase rates of predation on small mammals by birds (Flowerdew and Ellwood 2001). The bird populations themselves can shift in abundance and composition following deer-driven changes to the structure of the understory (McShea and Rappole 2000; Gill and Fuller 2007). These studies demonstrate that cervid herbivory can have far-reaching impacts on abiotic components and biotic communities.

Some of these impacts of cervid feeding may be mitigated by carnivores. The simplest model for these trophic cascades involves predators reducing prey numbers or biomass. This reduction in turn affects lower trophic levels. This type of cascade has been observed occurring in wolf-ungulate systems in the Quebec-Labrador peninsula (Crete and Manseau, 1996), where moose density was seven times higher in the absence of wolves. In undisturbed systems, apex predators have the potential to exert top-down control, limiting numbers of herbivores (Ripple and Beschta 2012). Evidence also exists that in some systems, predation risk effects, or the behavioral changes driven by predator
presence, can also drive trophic cascades. For example, wolves in Yellowstone National Park (YNP) may be influencing elk movement, foraging behavior, and browsing patterns, which in turn affect the recovery of quaking aspen by reducing herbivory in areas of higher risk (Ripple et al. 2001). Another study in YNP demonstrated that cottonwoods were taller and experienced lower browsing intensity in sites that were riskier, with low visibility and/or the presence of escape barriers like gullies (Ripple and Beschta 2003). Ripple and Beschta (2004) have also recorded reduction in browsing intensity on willows in some areas of YNP, which they believe is due to predation risk effects in conjunction with reduction in local elk numbers. The movement of cervids in the environment can also depend on predator habitat use: elk in YNP move preferentially into forest types that carry a lower risk of encountering wolves (Fortin et al. 2005).

More recent research in Wisconsin implicates wolf recovery as causing trophic cascade effects in the east as well. Wolf presence may be driving higher cover of forbs and shrubs and reversing some of the changes caused by deer (Callan et al. 2013, Bouchard et al. 2013). However, the mechanism of the effects is not known. It is unlikely that wolves in Wisconsin are having large-scale effect on deer numbers in the short term (Bouchard et al. 2013). The effects may instead be behaviorally-mediated, and studies of risk-sensitive behavior could be useful in determining potential driving factors of Wisconsin trophic cascades.

When we consider predation risk as a cost of foraging, we can understand behaviorally-moderated trophic cascades in the context of optimal foraging. Optimal
foraging theory (MacArthur and Pianka 1966) states that animals are selectively pressured to make foraging decisions that maximize energy intake per unit time and minimize costs. Animals must constantly make decisions in their environment, weighing costs and benefits of each activity. Often, the options that would make an animal a more efficient forager increase the risk of it becoming prey (Lima 1998). For example, spending less time being vigilant enables an animal to maximize time spent feeding, but in a risky environment, doing so may not be worth the risk of attack. As a result, herbivore foraging behavior varies with predation risk. Natural selection should thus produce animals that choose appropriate tradeoffs between risk of death by predation and intake of energy (Lima 1998).

One important decision that animals must make is how to use space when predators are present. On a broad scale, animals may proactively avoid predators by preferentially using areas that predators are less likely to use. For example, hedgehogs (Erinaceous europaeus) may use areas closer to buildings, where badgers (Meles meles) are less likely to be (Doncaster 1994). The “terrain fear factor” is a conceptual model (Ripple and Beschta 2003) that proposes prey species change foraging patterns and use of space according to terrain features and how much the features affect predation risk in the site. These behavioral effects can occur at a large scale, with prey animals proactively avoiding certain types of habitat. Bighorn sheep (Ovis canadensis), particularly females with young, prefer to feed in or near steep terrain over the flat and more lush valleys where they are more likely to be attacked by predators (Berger 1991). The effects of
particular habitat types on behavior also depend on the predator-evasion strategy of the prey animal. For example, in a study that determined perceived risk at sites in open, forested, and edge habitat, mule deer perceived a lower predation risk in open relative to forested areas (Altendorf et al. 2001). This perception is likely due to their tendency to avoid predation by spotting predators at a distance.

Foraging behavior may also depend on the risk of predation on a smaller scale. For example, when artificial seed patches were offered, gerbils (Gerbillus allenbyi) removed many more seeds from patches under protective bushes than those 1m from the bushes (Kotler et al. 1991). Because harvesting patches provides diminishing returns, the results reflect the point at which the rate of return is no longer worth the costs for the animal. The results of this study demonstrate that higher risk of predation away from bushes causes a reduction in feeding. In riskier open patches, gerbils are willing to leave a greater density of food behind because the rate of intake more quickly becomes insufficient to make up for the risks. Even at this smaller scale, the predator evasion techniques of species can also become apparent. Lima and Valone (1991) investigated microhabitat use among birds to see how microhabitat structure affects which species occur. When they manipulated habitat by adding bushes, the distribution of birds changed: birds that depended on cover to escape from predators became more common, while those whose escape tactics were independent of vegetative cover became less prevalent (Lima and Valone 1991).
These studies exemplify how fine-scale environment structure can impact animal behavior. This information can be meaningful for mitigating herbivore damage. Grizez (1960) demonstrated that slash, branches left behind from logging, can aid in forest regeneration by protecting seedlings from browsing by ungulates. Leaving behind woody debris, whether it is the result of logging, fire, or windfall, is considered a standard forestry management practice (Pellerin et al. 2010). Though a variety of studies have evaluated woody debris’ efficacy at protecting seedlings, the results have been inconsistent. Many studies found similar results to Grizez; that is, the woody debris reduced herbivory by ungulates (de Chantal and Granstrom 2007, Casabon and Pothier 2007, Hunn 2007, Relva et al 2009). Others, however, found that debris had no effect (Bergquist and Orlander 1998a, Kupferschmidt and Bugmann 2005, Frederickson et al. 1998, Krueger an Peterson 2009) or even increased herbivory (Pellerin et al. 2010, Bergquist et al. 2003). Whether woody debris is effective at reducing deer herbivory is likely dependent on the size and type of debris. Environmental factors such as habitat type and quality, light levels, and soil composition also likely play a role.

How slash protects seedlings is not yet clear. In some cases browsing still occurs on seedlings within slash, so it cannot always be that slash simply prevents deer from reaching seedlings (de Chantal and Granstrom 2007, Grizez 1960). One explanation for some cases is that feeding near slash piles increases the risk of predation for cervids whose predator-evasion strategy involves spotting danger from afar. Slash piles physically impede vision and may impede escape. A reduction of feeding in these riskier
areas would be in agreement with risk-sensitive foraging under the optimal foraging theory. Regardless of the manner of protection, hardwood forests of Wisconsin will benefit from retaining slash piles if the piles reduce browsing by white-tailed deer.

The effect of slash on forest regeneration is unclear and the mechanism or mechanisms by which it functions are not certain. Furthermore, few previous studies have tested hypotheses experimentally, measured deer behavior at slash directly, or examined the possibility of predation risk affecting the results. The purpose of this study was to experimentally investigate whether leaving slash in a northern Wisconsin forest was having a measurable effect on deer foraging behavior on a fine scale. I also aimed to identify whether risk-sensitive foraging could explain such a pattern. I had three main objectives during the course of the experiment. First, I directly measured browse intensity on sugar maple seedlings adjacent to/within slash as well as in the open to test the hypothesis that deer were foraging less within the slash. The browsing of deer who are foraging optimally should balance costs related to foraging with the energetic intake (Brown 1988). Animals foraging under higher risk will make decisions to reach a balance between energetic intake and foraging costs. They may leave riskier patches sooner or use the patches less in general. A difference in browse intensity here may therefore reflect a difference in perceived predation risk between slash and open plots. I also established food trays to determine whether deer given identical food sources vary their foraging behavior based on proximity to slash. Finally, I measured vigilance levels throughout the study area to assess whether deer are hyper-vigilant in slash-heavy areas.
II. METHODS

STUDY AREA

I conducted this study in a tract of sugar maple-dominated northern hardwood forest in Vilas County, Wisconsin, in the summer of 2014. The land is owned by Dairymen’s, Inc, an organization with focus on low-impact recreation and stewardship. Vilas County is within the Northern Highlands region and has a continental climate. Glacial deposits dating from the Pleistocene form moraines and outwash plains in the area, and the Dairymen’s property includes oligotrophic drainage lakes, forests, and wetlands (Rooney 2009).

I conducted this study in a portion of the forest, located northwest of Wolf Lake (near 46°10'09.5"N, 89°40'06.0"W), which had been thinned 1 year prior. Slash piles, or groups of large branches left behind after logging, were scattered throughout the area with spacing that varied anywhere from less than 10m to more than 40m between them (Figure 1).

White-tailed deer in the area occur at a density of roughly 10 individuals/km², down from a peak of approximately 14/km² in the 1930s and ‘40s (Alverson et al. 1988). Grey wolves (Canis lupus) began returning to Wisconsin in the mid-1970s, with wolf presence at Dairymen’s likely beginning again in the mid-2000s (Wydeven et al. 2009).
BROWSE PRESSURE SAMPLING

I established browse pressure sampling plots ("tree plots") 13 May 2014, creating forty total plots in a paired design. To create the plots, I haphazardly dropped a 1x1m quadrat, with 1 plot in each pair flagged adjacent to a slash pile ("slash" treatment) (Figure 2) and a control flagged 10m away in unobstructed ground ("open" treatment). I established these pairs of plots approximately 50m away from one another.

When the corners of the plot had been flagged, I scattered 15g of Scott’s Turf Builder 32-0-4 fertilizer by hand throughout the plots. On 3 June, I added 40 additional grams of fertilizer to each plot. I added high-nitrogen fertilizer to increase stem nitrogen in seedlings, to make the seedlings more attractive to deer (Tripler et al. 2002) and decrease my chance of failing to find an effect through lack of foraging.

To measure browse pressure on maple seedlings, I used the Sugar Maple Browse Index (SMBI), a method originally described by Frelich and Lorimer (1985) and modified by Rooney et al. (2000). This method involved counting all leaves on a seedling as well as how many of the leaves were clipped off from browsing. The percent of browsed leaves functions as an indication of browse intensity. To calculate and compare browse intensity in slash plots and open plots, I calculated the percent of leaves browsed for 10 random seedlings per plot, as chosen by random number generator.

I took the first round of browse index measurements from 3 June to 4 June and marked seedlings with a paint marker to find them again throughout the experiment. When I could not find a marked seedling at a later date, I noted this and instead took
measurements from a new tree as near to the location of the original as possible. I took follow-up browse index measurements on 24-25 June and 7-8 August. Most seedlings measured were small, generally 20cm or less, though some were up to heights of approximately 50cm.

GIVING-UP DENSITY SAMPLING

I measured giving-up density from 6 June to 26 June. Giving-up density (GUD) is an alternate way of measuring foraging behavior at a small scale. Food patches with a set density or weight of food are established to measure the point at which animals make a decision, based on costs and benefits of foraging, to “give up” and move on. An animal that perceives fewer benefits or greater costs to foraging at a particular patch will give up on that patch sooner, leaving a higher density or weight of food behind. Measuring GUD using a valuable food source provided me the opportunity to measure foraging behavior in a controlled way. This method also eliminated differences in energetic costs of foraging in slash and open plots.

To measure giving-up densities, I built 20 food trays from plastic shoeboxes (13" x 7-1/2" x 4-1/4"), and added 2 x 3” wire across the tops. The wire prevents deer from shoveling out the tray contents. I drilled a pair of holes in the bottom of each to allow two 8.5cm nails pass through and anchor in the ground.

I filled these trays with a mixture of 400g medium sized bark chips and 100g of whole corn. Bark chips were not terribly absorbent and could be mixed fairly well with
corn. After filling, I placed trays 1m from each browse plot in random established pairs. I removed remaining corn daily and weighed it, dried it at 165 degrees Fahrenheit for 24 hours, then weighed again to correct for water weight gained from humidity and rain. I added a new 100g batch of corn to each tray daily. The weight of corn remaining after each night represents the “giving-up density”, or the amount of food left in a plot at the point that an animal gives up and moves on to another foraging patch.

VIGILANCE SAMPLING

I recorded activity around plots and use of plots with trail cameras placed at randomly assigned paired plots. I placed eight cameras total: four Leaf River DC-1BU's and four Reconyx Hyperfire cameras that use a passive infrared motion detector. I assigned half of the cameras to face browse plot pairs while the others faced food tray (GUD) plots. When possible, I attached cameras facing northward to prevent light interference.

I strapped cameras to trees at approximately waist to breast height and angled them slightly downward toward plots, testing to ensure proper placement before sampling. The distance from plot to camera varied because of tree locations, but generally was between 5 and 12m. I kept the cameras set up continuously from 3 June to 8 August.

Due to a lack of usable photos, I was unable to compare the vigilance of deer at control and experimental plots. Instead, I measured overall vigilance across the study.
site, by comparing numbers of vigilant and non-vigilant deer in photos. I considered it “moving vigilance” when a deer was in motion, but held its head horizontally or higher, with ears perked forward, and “still vigilance” if the same behaviors were occurring but the deer was not walking or running. I categorized all other behaviors as “non-vigilance.”

I also calculated the number of deer per camera night as an index of deer population in the area. Because the Leaf River cameras were less reliable, I excluded them from this analysis, leaving me with 144 camera nights (four cameras running for 36 days). I then counted each individual deer caught on these four cameras to estimate the number of deer found per camera night.

DATA ANALYSIS

BROWSE PRESSURE

I analyzed differences between browse pressure in open and slash treatment tree plots using a replicated G-test of goodness of fit in the R statistical program. I calculated expected percent of browsed leaves for each pair of plots. Using these values, I conducted G-tests for each individual plot and then found the total, pooled, and heterogeneity G.

To test whether there was a difference in the number of total leaves in open areas versus slash I conducted a G-test goodness of fit using the same methodology as described above. I calculated expected values for total leaf numbers in each pair of plots.
Using these values, I then conducted the G-tests for each plot individually before finding the total, pooled, and heterogeneity G. Because ten seedlings were sampled in each plot, leaf number acts as a proxy for seedling size. Conducting this test reveals whether seedlings in and out of slash differed in size. A difference in average seedling size may impact deer foraging decisions.

To rule out the possibility differences between slash plots and open plots could be an artefact of sample size, I performed a post-hoc power analysis. Specifically I used logistic regression analysis with the number of leaves per pair of plots as the independent variable. The dependent variable was binary, and coded as statistical significance at the $P < 0.05$ level for each of the 20 pairs of plots (significant, not significant).

GIVING-UP DENSITY

I conducted a standard one-way ANOVA to analyze GUD data and determine whether amounts of corn left behind in plots were significantly different between open and slash treatment trays.

VIGILANCE

To measure vigilance rates, I pooled the still and moving vigilance photos. I then found the percent of photos taken in which the deer was vigilant.
I also counted photos displaying other animals using the study site, and examined the proportion of animal photos taken of each species to see what animals were using the study site and how often.

I conducted a G-test of goodness-of-fit to test the hypothesis that the proportion of vigilant deer photos taken during the day differs from that at night. I expected deer to be more vigilant at night, because they would be unable to see as far and would likely have more difficulty navigating past slash in the darkness.
III. RESULTS

BROWSE PRESSURE

The mean ratio of browsed to unbrowsed leaves in open plots (0.066 ± 0.015) was almost twice of that in slash plots (0.037 ± 0.012, Figure 3). This difference is significant (Table 1). The effect varied from paired plot to paired plot (G heterogeneity, df=19, P < 0.001). However, the tendency was usually for a greater fraction of stems browsed in open plots.

The mean number of maple leaves in open plots (43.75 ± 5.16) was significantly greater than in slash plots (38.65 ± 2.56, G-test, df=1, P<0.001).

Post-hoc power analysis indicated that the observed statistical significance at the paired plot level was not a function of the number of leaves present (0.01082 ± 0.01765, z = 0.613, P = 0.54, Figure 4).

GIVING-UP DENSITY

Contrary to expectations, the mean dry weight of corn left in slash plots each day (the GUD) (35.26 ± 2.55) was not significantly different from open plots (41.97 ± 2.83) (one-way ANOVA, F=3.1, P = 0.079, Fig 4).
VIGILANCE

The mean proportion of photos of vigilant deer taken during the day (0.20 ± 0.05) and night (0.23 ± 0.05) did not differ significantly (G-test, df=1; P = 0.1381).

Of 207 usable deer photos, 17% depicted vigilant behavior. Daytime photos made up 59% of all deer photos. Among photos capturing animals, 74% captured deer and 23% raccoons (Table 2). The remaining photos included 3 of an opossum (*Didelphis virginiana*) and 6 of a coyote (*Canis latrans*).

I counted a total of 53 individual deer photographed by the Reconyx cameras over 144 camera days, or approximately 36.8 deer per 100 camera days.
IV. DISCUSSION

BROWSE PRESSURE

The results of the browse pressure experiment demonstrate a nearly 50% reduction in the proportion of leaves browsed in or directly adjacent to slash piles. This finding is in agreement with a number of previous studies that found slash beneficial for reducing browse intensity (Grisez 1960, de Chantal and Granstrom 2007, Casabon and Pothier 2007, Hunn 2007, Relva et al 2009), though it is contrary to some studies that found no effect (Bergquist and Orlander 1998a, Kupferschmidt and Bugmann 2005, Frederickson et al. 1998, Krueger and Peterson 2009) or even an increase in browsing caused by woody debris (Pellerin et al. 2010, Bergquist et al. 2003). The results suggest that in the northern hardwood forest of Dairymen’s, Inc, retaining slash after logging can help protect maple seedlings from deer herbivory and promote forest regeneration.

We must consider two questions regarding slash’s effect on herbivory: at what scales does the effect occur, and what drives the changes? On a fine scale, slash may directly protect seedlings so “open” areas in the vicinity experience heavier browse damage. But on a broader scale, slash may create an entire site that deer browse less intensely. In this way, slash could indirectly protect vegetation in its vicinity.

I investigated slash at a fine scale, comparing browse levels within slash to browse levels in open areas of the same site. The fact that I found a significant difference in browse intensity within the slash demonstrates that the woody debris is directly
protecting the seedlings within and immediately around it. This finding does not exclude a site-wide reduction in browse as a co-occurring phenomenon.

My results show reduced herbivory in slash compared to adjacent areas; similar results have been found in other studies comparing slash to adjacent areas (de Chantal and Granstrom 2007, Grisez 1960). Grisez (1960) found that while 36% of trees in slash were browsed, 51% out of it had browse damage. De Chantal and Granstrom (2007) found even more dramatic effects. For quaking aspen (*Populus tremula*) 83% suffered browsing in open plots, but only 11% in slash, and pussy willow (*Salix caprea*) seedlings were subject to a similar effect, with 97% and 20% browsed in open and slash areas respectively.

The reason for the reduction in browse within slash at this scale must still be considered. The most obvious conclusion is that slash simply acts as a physical barrier, blocking deer from accessing leaves. In my study, that mechanism cannot explain the results. Browsing still occurred, and I established unobstructed quadrats to allow accessibility. Yet another explanation for the browse reduction is one of convenience and energetics. Although seedlings in slash were accessible, the presence of the slash may present a considerable obstacle for foraging. If slash is difficult for deer to navigate, browsing seedlings within it will be more energetically costly than browsing nearby seedlings in flat, unobstructed ground. This explanation is also in accordance with optimal foraging theory, because a greater energetic cost of foraging should also cause deer to reduce browsing at slash plots. However, this effect could be independent of
predation risk. To identify whether risk-sensitive foraging is part of this system, I would like to conduct trials using deer populations under high and low predation risk. I would also prefer more comprehensive measures of behavior around slash piles to determine whether deer increase vigilance or search time during foraging in slash.

Another possibility is that slash shades seedlings or otherwise makes them less vigorous than those receiving full sun in the open. This greater vigor in open-plot seedlings would make them more appealing to herbivores and more prone to browse damage, as per the plant vigor hypothesis (Price 1991). Two observations suggest that differences in vigor do not explain my results. There were more leaves in open plots than slash plots, but differences among plots were highly variable. Four sites had significantly more leaves in control plots, and 3 sites had more in slash. Therefore, it is unlikely that observed patterns reflect deer selecting feeding patches with a higher number of available leaves. The fertilization of all plots with nitrogen should also have made both slash and open plots attractive to deer. Sugar maple seedlings can use extra soil nitrogen, increasing their stem nitrogen content (Tripler et al. 2002). Deer are known to browse such high-nitrogen seedlings of many species at a greater rate (Tripler et al. 2002). In this study, the seedlings in established plots were often a visibly richer green than surrounding seedlings, suggesting a greater nutrient content (Figure 5). Therefore, both slash and open plots had vigorous seedlings whose number of leaves did not vary consistently by treatment. Because vigor was similar, I can assume vigor was not related to the reduction in herbivory by slash.
Although my results show that slash can reduce browse pressure, the cause of the reduction remains unclear, and more research is necessary to determine at what scales slash effectively protects seedlings in this system. Because studies on herbivory and woody debris vary widely in the type of woody debris studied, the density of such debris in the site, the methods of measurement, and the scale of consideration, making comparisons to other research can be difficult. Identifying the cause of reduced herbivory in any given system will likely require an approach that takes deer behavior into account as well.

GIVING-UP DENSITY

I found no significant difference in the mean weight of corn left in open and slash plots each day. Although the difference did not reach significance, the slash plot trays had slightly lower GUDs on average, contrary to the expected trend.

The giving-up density portion of the experiment suffered from demonic intrusions (Hurlbert, 1984) in the form of raccoons. Throughout this portion of the experiment, trail cameras detected raccoons frequently attending the food trays. Often, I would find trays the following day that had been pulled out of the ground despite their nail anchors and then strewn about. Raccoons sometimes pushed the wire coverings down several centimeters to reach all the corn. Once I completed the GUD portion of the experiment, raccoons no longer appeared, demonstrating their ability to learn to return to food sources and quickly abandon them when they become unavailable. This learning ability has been
documented before and is beneficial for taking advantage of ephemeral food sources under natural conditions (Dalgish and Anderson 1979). It is likely that rodents such as chipmunks, which like to use slash piles for cover (Borreco 1976), were also eating the corn but were too small to trigger the trail cameras. I occasionally observed them within the slash piles.

Other researchers have had success using food trays to measure GUD in ungulates without suffering from such intrusion (Altendorf et al. 2001, Kotler et al. 1994). When demonic intrusion is likely, the methods should be tested for their ability to exclude unwanted visitors. The structure of feeding trays could be modified, though allowing for deer to feed while excluding smaller animals is a challenge. This problem is especially difficult when food trays cannot be elevated; in this study, allowing deer to eat from elevated trays may have mitigated the effects of slash as an obstacle to vision and escape. A more species-specific bait could also be used to avoid attracting other animals. For example, trimmed branches or nitrogen-fertilized potted plants are attractive to deer but are unlikely to be used by many other species. A known number of leaves on such plants is usable in place of a known density of corn. Alternatively, deer could be directly observed and giving-up time measured in place of giving-up density.

VIGILANCE

I calculated vigilance levels throughout the study site and found around 17% of deer photos depicting vigilance behavior. This rate did not vary by day and night,
suggesting that despite reduced vision, deer perceive a similar risk at night. Determining whether their vigilance level is high or low will require more research in areas around the study site. Comparing to other studies is difficult because vigilance levels can vary drastically. For instance, in a study in North Carolina, single deer spent more than half their time vigilant at all times of day (Lashley et al 2014), while research done in Kansas found that single deer spent only 9.83 (± 7.97)% of their time vigilant (Lark and Slade 2008). If the vigilance level is low relative to surrounding forest, the data suggest predation risk at the study site was comparatively low.

Low vigilance may also suggest that deer need to maximize energy intake. Wisconsin’s Department of Natural resources rated the winter of 2013-2014 as very severe (WiDNR 2014). Deer in the study site may have been spending more time feeding to mitigate fat losses from a harsh winter. Furthermore, a lack of human hunters can also reduce vigilance levels in deer (Benhaiem et al. 2008). Dairymens, Inc. does not permit hunting, so the deer in this area have not been at risk of death by humans for many years.

Originally, my intention when measuring vigilance was to investigate it at the same fine scale as the rest of the study and compare vigilance at plots by slash to vigilance away from it. Because the majority of deer photos were of animals passing by rather than using sites, and because the position of deer in photos varied greatly and could not be accurately categorized as “by slash” or “in the open,” I calculated site-wide vigilance instead. Unfortunately, this difference of scale makes the vigilance data difficult to compare to the rest of the study. That difference bars concluding that an
increase in vigilance causes the reduction in browse intensity. However, useful
information may still be gleaned from the vigilance data even at this broader scale,
though the usefulness of the vigilance data will surely increase with more comparative
data being gathered.

Deer photos were categorized as “day” and “night” fairly easily because very few
photos were taken in low light at the beginning or end of the day. This lack of dusk and
dawn photos may reflect deer behavior under predation risk as well. Because wolves are
typically crepuscular (Merrill and Mech 2003), deer may be responding to predation risk
at those times by simply avoiding the study site entirely, rather than by being more
vigilant. This action is a type of proactive anti-predator behavior, as opposed to reactive
behaviors like increasing vigilance. Though avoidance of high-risk areas does occur
(Ripple et al 2001, Fortin et al 2005), some researchers found that deer do not always
avoid high risk areas and may instead alter their behavior at risky sites (Kittle et al.
2008). Again, more comparative data are needed.

The presence of coyotes in the study site may also imply that this site is not under
heavy use by wolves, as coyote densities tend to be lower in the presence of wolves
(Ritchie and Johnson 2009). Wolves are present in the general area, and another
researcher found both scat and tracks of wolves 1.5 meters from the study site a few
months prior to my work (Rooney, personal correspondence). I did not find signs of
wolves. However, since wolves and coyotes are known to have overlapping territories
and coexist at times (Arjo and Pletscher 1999), I cannot conclude with certainty that
wolves are not using this particular area. A further study could investigate whether the effects of slash on deer herbivory are increased in areas that are frequented by wolves versus areas without wolves, which could also help identify whether predation risk is related to reduced browsing near slash.

FUTURE RESEARCH

This experiment opens the doors to future research possibilities. Further experiments into the mechanisms by which slash protects trees could illuminate how it can be used best. Researchers could, for example, investigate at what scales slash is effective, in what habitat types it works, and what types of debris are most useful. Many features of woody debris, from its size, and type to its spacing, may affect its effectiveness at protecting tree seedlings.

For example, researchers should clarify the scale at which the study is being done so that the scale of effectiveness can be considered. This study demonstrated that at a fine scale, tree-top slash may reduce browsing adjacent to and within slash versus immediately nearby open areas. However, other studies have found that browse pressure may be reduced in areas with slash versus areas without (Casabon and Pothier 2007, Hunn 2007, Relva 2009, Bergquist and Orlander 1998a, Frederickson 1998, Pellerin et al 2010, Bergquist et al 2003). If a reduction in herbivory occurs at a broader scale, it would be valuable to compare the strength of this effect to that of the fine-scale browse reduction. If browsing drops much more heavily at a small scale, increasing levels of
slash should promote forest regeneration. However, if the browse reduction is more effective at a broad scale, there may be an optimal spacing of slash, after which a change in spacing does not significantly decrease browsing. Therefore, studying broad-scale slash effects at different densities and sizes of slash may also be useful.

The spacing of the slash piles (generally 10-40m apart) may also impact deer behavior. The “open” areas in this study were generally spaces between slash. Narrow slash spacing may impact site-wide vigilance levels. To identify whether vigilance levels actually vary due to density of slash, future studies could investigate deer behavior and browse intensity at different spacings of slash to see whether browse intensity increases with distance from slash.

The size of slash must also be taken into consideration. If creating fewer, but larger piles of slash is more beneficial than small numerous piles, such information could be valuable to the forestry industry. Other researchers have found that a greater height of slash can increase the benefit to young trees (de Chantal and Granstrom 2007).

In addition to features of the slash itself, the effects of retaining woody debris on browse intensity can depend on environmental factors like habitat type as well as light level and soil composition (Pellerin et al. 2010). In some cases, woody debris can create particularly favorable microhabitat for seedlings (Pellerin et al. 2010) or fertilize them through the decay of plant material (Bergquist and Orlander 1998b). In poor quality habitats, seedlings in such areas may be particularly attractive or visible to deer, resulting in higher browsing rates than on other seedlings (Pellerin et al. 2010, Bergquist et al.)
Certain types of woody debris, like rotting logs, may also be more likely to create this scenario (Pellerin et al 2010). My study site was not poor habitat, and was fairly well carpeted with sugar maple seedlings. Furthermore, woody debris in the study site was relatively fresh slash rather than moist, decaying plant matter. Coupled with the finding that slash plots did not contain more stems, this information suggests that slash in my site is not creating moister or more fertile microsites.

Follow-up studies in my study site could investigate whether the effect of slash changes as seedlings grow to saplings of sizes that deer more typically prefer. The trees I measured were new seedlings, many of whom only had two leaves besides their cotyledons at the first measurement of browse intensity. Deer tend to prefer somewhat larger seedlings and saplings over smaller size classes (Rooney et al. 2000, Waller et al. 1997, Kittredge and Ashton 1995, Tilghman 1989). The effects of slash may vary based on the size class of the trees as well as their species. In some cases, the effects from the removal or leaving of slash may not even be apparent until 5 years or more after logging (Bergquist et al 2003), and my study site had only been logged the previous year. Continuation of measurements may reveal an effect that grows over time. If slash is already reducing browse damage, the slash seedlings could more quickly grow to heights that would protect them from deer herbivory (roughly >1.5m) (Tilghman 1989) and the difference in browse pressure may become more obvious.

Regarding behavior, future studies should attempt to measure vigilance at a fine scale, comparing vigilance by slash to areas immediately adjacent. Doing so could reveal
whether fine-scale foraging decisions explain browse reduction by slash. Given the difficulty of such fine-scale measurements, direct observation of deer behavior at sites may also be beneficial. To assess whether deer qualify as foraging by slash or away from it, areas around slash could be marked in chalk or flour. Although cameras save time, preliminary experiments should be conducted to assess their usefulness for the study. In addition to vigilance, search times for leaves could also be counted to address whether reduced herbivory is related to an increase in time and energy costs instead of an increase in risk.

Use of food trays to measure GUD must be improved or replaced by measurements of giving-up time. Using these methods alone or in conjunction with cameras or marking off slash may be successful. The use of food trays is valuable to the study of slash because it eliminates potential differences in search times in and away from slash, allowing for researchers to exclude that as an explanatory variable.

Ultimately, whether slash works at reducing deer herbivory is a complex question that depends on a wide variety of interconnected variables. Standardized methods of measure makes studies more easily comparable. Researchers should strive toward detailed descriptions and thorough methods, as well as keep both scale and causative factors in mind when designing studies. Identifying the scale and conditions at which slash is beneficial, as well as the mechanisms that make it so will be the biggest steps toward maximizing the usefulness of woody debris in forest regeneration. My study
represents some of the earliest research that measures browse in slash experimentally at a fine scale and attempts to understand the effects by measuring deer behavior.

CONCLUSIONS

My study reveals some of the earliest experimental evidence of slash’s ability to protect seedlings from browse damage by ungulates on a fine scale. Because browsing still occurred, I can conclude slash does not prevent browsing but impacts deer foraging behavior.

This study is also one of the first to attempt to explain benefits of slash in forestry by measuring deer behavior around slash. The low levels of crepuscular activity detected suggest that deer may use proactive antipredator behaviors in this particular study site. Whether the reduction in browse is the result of risk-sensitive foraging was not verified by this experiment, but further researchers could address this question by measuring vigilance in real time and by tracking changes in browse intensity and deer behavior at different scales. Ultimately, more research on slash will help the forestry industry maximize its effectiveness at mitigating damage by white-tailed deer.
V. REFERENCES


63. WisDNR. 2010. White-tailed Deer Population Status 2010. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

64. ___. 2015. 2013-2014 Winter Severity Index. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

VI. FIGURES AND TABLES

Figure 1: Slash piles in the area of the study.
Figure 2: A slash plot at the time of establishment.
Figure 3: The ratio of leaves browsed to unbrowsed on maple seedlings in slash-adjacent and open-ground plots in northern Wisconsin. The means are significantly different (G-test, df=1; P < 0.001). For slash, outliers are greater than 1.5 times the interquartile range and whisker represents the highest value less than that. Slash values are as follows: maximum = 0.22, whisker = 0.09, Q3=0.05, median = 0.02, Q1 = 0. Open values are: maximum = 0.19, Q3=0.13, median = 0.38, Q1 = 0.
Figure 4: Logistic regression analysis with the number of leaves per pair of plots as the independent variable. The dependent variable was binary, and coded as statistical significance at the $P < 0.05$ level for each of the 20 pairs of plots (significant/not significant).
Figure 5: The mean dry weight of corn (g) left over after each day (GUD) in slash-adjacent and open-ground plots in northern Wisconsin. The means are not significantly different (ANOVA, F=3.1, P=0.079). Slash values are as follows: maximum = 114, Q3=76, median = 14, Q1 = 3, minimum = 0.5. Open values are: maximum = 114, Q3=91, median = 20, Q1 = 3, minimum=0.
Figure 6: Slash plot in August. Note the relative darkness of seedlings within the plot, demonstrating their higher stem nitrogen level.
Table 1: G-test of goodness of fit, testing the hypothesis that proportion of browsed and unbrowsed maple leaves does not differ between plots established adjacent to slash and those established in open ground. For P values, * indicates P ≤ 0.05, ** indicates P ≤ 0.01, and *** indicates P ≤ 0.001.

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43
Table 2: Photo count data from trail cams. Odd-numbered cams represent slash treatment plots. “Other” animals were an opossum (camera 19, 3 photos) and a coyote (camera 20, 6 photos). Cameras 9, 10, 33, and 34 were Leaf River cameras. The others were Reconyx Hyperfire.

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