Effect of Bird Predation and Nutrient Input on a Mixed-Grassland Trophic Cascade

BIOS 35502: Practicum in Field Biology

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Abstract

Trophic interactions between avian predators, phytophagous herbivores, and plant communities vary across ecosystems. In most cases, avian predators control insect populations and therefore assist plant growth. Grasslands comprise over a third of all terrestrial ecosystems and, via various forms of succession, are constantly changing in species and nutrient composition. This succession can be either accelerated or inhibited by trophic interactions. This study sought to determine how herbivory in a successionary grassland field surrounded by a forest ecosystem was affected by avian predation and nutrient input. Bird exclosures were set up randomly throughout a field, and half were then fertilized with nitrogen. Estimates of herbivory were the measured at each plot and compared to plots without exclosures or fertilizer in order to assess the effects of predation and nutrients on insect feeding habits. Excluding predation led to increased levels of herbivory, while nutrient input showed no effect on insect feeding. These results suggest that top-down effects play a large role in the structure of mixed grassland ecosystems. Systems undergoing succession such as this should be aware of the effects of both predation and neighboring ecosystems on overall ecosystem composition and function.

Introduction

Almost 40% of accessible terrestrial ecosystems can be classified as grassland ecosystems (White et al 2000). Grasslands comprise a vital habitat for many different types of organisms. Many of the interactions between inhabitants of these complex ecosystems have been studied extensively as a part of the trophic cascade theory (Halaj and Wise 2000). Trophic cascade theory postulates a response of one level of a food web due to a change in another level, even if there is no direct predatory or herbivorous connection between the two. For example, studies of wolf reintroduction have found that adding wolves, a predator of deer, to an ecosystem, increases the total amount of vegetation in forests (Ripple and Beschta 2008). This is because deer under predation pressure spend more time watching for predators and less time feeding. In this case, the addition of a predator to the top of the food web had an impact on plants, the base of the food web (Ripple and Beschta 2008). This ability for the impacts of a higher order predator to trickle down to lower order plant communities is an example of a top-down cascade.

Similarly, bird and insect interactions can also have a large impact on overall ecosystem health and function through trophic cascades (Halaj and Wise 2000). Insects are an important link in trophic cascades, as they are the primary food web connection between birds and plants (Marquis and Whelan 1994, Pin Koh 2008). If bird populations decrease, there is potential for a decrease in the overall predation of insects, which could lead to increased herbivory, thus stunting plant populations. Alternatively, an increase in bird activity could reduce insect populations, causing a decrease in herbivory and increased primary production.

Previous studies in forest ecosystems have attempted to analyze this relationship between predators, herbivores, and plant communities (Tscharntke 1992, Marquis and Whelan 1994, Beckerman et al 1997, Rosenheim 1998, Giffard et al 2012). Many of these studies have focused on the effects of intraguild competition at various trophic levels. Increased intraguild competition between predators for herbivore prey, as well as between herbivores for plants, has been shown to cause changes in overall ecosystem composition and limit the cascade of trophic effects (Rosenheim et al 1993, Rosenheim 1998, Finke and Denno 2006). However, it has been shown that, in most cases top-down or bottom-up influences are more responsible for ecosystem-wide population dynamics than interspecific competition (Tscharntke 1992, Marquis and Whelan

1994, Beckerman et al 1997, Schmitz et al 1997). Effects due to predation largely outweigh the effects of competition in these large-scale ecosystem studies.

Additional studies have sought to weigh effects of predation against the behavior of various prey species in order to assess the drivers of this trophic relationship and to explain changes in herbivory in the presence of increased predation (Holmes et al 1979, Schmitz et al 1997, Beckerman et al 1997, Rosenheim 1998, Denno et al 2002, Finke and Denno 2005, Giffard et al 2012). In one study, insects that perceived a threat of potential predation and changed some behavior in response (Schmitz et al 1997). Their increased levels of vigilance also lead to changes in their amount of herbivory on plant populations, showing how predators are helpful at maintaining a balance in the food web (Holmes et al 1979, Altegrim 1989, Bruns 2009).

Despite being an important ecosystem, trophic cascades in evolving grasslands are still relatively understudied compared to those in forest ecosystems (Joern 1986, Pin Koh 2008). Research focusing on succession of grasslands has found that birds can help facilitate succession by controlling herbivorous insect populations (Joern 1986, Altegrim 1989, Marquis and Whelan 1994, Beckerman et al 1997, Strong et al 2000). Alternatively, excessive herbivory by insects has been shown to slow the process of succession (Carson and Root 1999, Fagan and Bishop 2000). Since insects selectively eat plants that provide stronger nutritional quality (Jonas and Joern 2008, Loaiza et al 2011), they artificially select for certain species. Previous studies have shown that nutrient levels are usually higher in earlier stages of succession (Uriarte 2000), making this artificial selection one reason for the slowed process of succession.

In spite of all this research on grassland ecosystems, it is not known precisely how insect populations respond to bird predation in successionary grasslands or in those surrounded by a different ecosystem, such as a forest. Additionally little is known regarding how this response affects rates of herbivory through a potential trophic cascade.

Insect herbivory is not only influenced by predation, but also by preferential selection of high quality food resources. Nutrient composition varies across plant species, and insects have been shown to select many food sources based on their nutrient composition (Jonas and Joern 2008). Nitrogen has been shown to be a limiting yet preferential nutrient in many late successional grassland ecosystems (Fagan and Bishop 2000, Uriarte 2000, Loaiza et al 2011). Studies have shown the presence of insect herbivores decrease the availability of nitrogen due to their preference for plants containing higher ratios of nitrogen (Uriarte 2000). However, there have been very few published studies regarding how this affects the relationship between insects and both predation and succession.

This study sought to combine a number of factors, previous studies, and understudied hypotheses in order to determine how herbivory in an early successional grassland field surrounded by a forest ecosystem is affected by avian predation and nutrient input. Much of the animal community located in the field of study are predominantly found in the surrounding forest, making it a mixed ecosystem and an ideal site to study both species interaction and succession. Organisms in this particular grassland may therefore be better adapted to top-down patterns similar to those found in forest ecosystems, which could potentially cause differences in the overall ecology of this grassland system (Joern 1986). By excluding avian predators and adding fertilizer to portions of a grassland field and analyzing how that changed herbivory, I attempted to draw a better picture of food web interactions in a setting. Specifically, I hoped to understand how forest predators have adapted to this mixture of forest and field characteristics in order to better utilize their environment.

I hypothesized that predation and fertilizer would affect levels of herbivory in two different ways. First, excluding birds from portions of the field would increase the amount of insect-driven herbivory, as there is less risk associated with feeding (Beckerman et al 1997, Schmitz et al 1997). Second, I predicted that increasing nutrients would also increase herbivory, as insects would select for higher nutrient content while feeding (Jonas and Joern 2008, Loaiza et al 2011). Additionally, due to the later successional stage of the field I predicted that predation would have more of an effect on herbivory, and therefore there would be more of an effect on herbivory in exclosures than in fertilized plots. I expected that exclosures with added nitrogen would show the highest amount of herbivory, while plots that lacked nutrient input and had no protection from avian predation would should the least amount of herbivory.

Methods

Study Site

This study was conducted at the University of Notre Dame Environmental Research Center (UNDERC-East) in Northern Wisconsin (41^{o}14.53 N, 89^{o}33.27 W) in a transitioning grassland meadow. The field where this study was conducted is irregular in shape (Figure 1), with a maximum length of approximately 182 meters and a maximum width of 109 meters. It is dominated by grasses, ferns, and a few select forb species.

This field was previously a fishing village until it was purchased by the University of Notre Dame, who has since left it unmanipulated. It is currently undergoing succession and may eventually assimilate into the surrounding forest. As it is surrounded by a lake on one side and forest on all other sides, it is utilized mostly by forest animals, including bears, foxes, deer, and forest birds including Red-eyed Vireos, Black-throated Green Warblers, Common Yellowthroat

Warblers, White-throated Sparrows, Black-capped Chickadees, Chipping Sparrows, and other species.

Experimental Setup

Twenty-four plots of 3 meters by 3 meters were randomly set up throughout the field (Figure 1). Bird exclosures approximately 36 inches in height were constructed with deer netting on 12 plots. The deer netting was small enough to prevent birds and other small predators from entering the plots, but was large enough to allow large insects to pass through freely. The final 12 plots were used as control.

Six control plots and six exclosures were fertilized with 10 grams per square meter of nitrogen (10 g/m^2 N) approximately three weeks after initial construction of exclosures. Fertilizer was applied using a block design by grouping two plots without exclosures and two with exclosures in similar areas so as to control for potential edge or environmental effects (Loaiza et al 2011, Joern 2013 personal communication). All plots were then left to grow for another 2.5 weeks for a total study length of approximately six weeks.

Bird point counts were taken throughout the season to determine bird species present. Additionally, sweep net samples were taken of insects to assess which phytophagous herbivores were present in the field.

Data Collection and Analysis

After approximately six weeks from the construction of exclosures, herbivory was estimated in all plots. Leaf damage was used as a proxy for herbivory (Loaiza et al 2011, Joern 2013 personal communication). Grasses were randomly selected and leaf damage estimated on a scale of one to four, where 1= 0-25%, 2= 25-50%, 3= 50-75%, and 4= 75-100% of the leaf missing. One hundred grass samples were estimated per plot and then averaged for a total of 24 plot herbivory indices. Herbivory was then compared between plots with and without exclosures, as well as between fertilized and non-fertilized plots using a blocked 2-Way Analysis of Variance.

Results

Bird species found in point counts in the field included Red-eyed Vireos, Black-throated Green Warblers, Common Yellowthroat Warblers, White-throated Sparrows, Blackcapped Chickadees, and Chipping Sparrows. Herbivorous insects were composed primarily of the orders Orthoptera and Lepidoptra. Orthopterans present in the field included those from subfamilies Conocephalinae, Atlanticus, Acrididae, Oedipodinae, and Cyrtacanthacridinae. The most abundant Lepidopteran found was a larval form of the subfamily Hesperrinae.

Plots with and without exclosures showed a significant difference in herbivory ($F=17.84$, $df=1$, $p<0.001$). Exclosures showed higher levels of herbivory in all plots than in non-exclosed plots (Table 1). Presence or absence of fertilizer did not show a significant effect on the amount of herbivory experienced in plots ($F=0.027$, $df=1$, $p= 0.41$) (Figure 2). There were no significant geographic effects from blocking on herbivory levels ($F=1.88$, $df=5$, $p=0.16$)

Discussion

Based on these results, I was able to accept one of my hypotheses. Herbivory of grasses was more affected by the absence of avian predation than by the input of nitrogen. Birds seem to be having enough of an impact on insect populations or behavior to limit the amount of herbivory experienced on species sampled, thereby potentially affecting the composition of the local plant community. This agrees with previous trophic cascade research from other studies (Tscharntke 1992, Marquis and Whelan 1994, Beckerman et al 1997, Rosenheim 1998).

The effect of the exclosures could be due to a variety of reasons. Studies have shown that the mere presence of a predator can be enough to limit feeding by some species (Beckerman et al 1997, Schmitz et al 1997). Prey are more likely to increase vigilance and practice cautionary behavior when there are predators present and are therefore likely to spend less time eating. Exclosures could have provided sufficient protection to limit vigilance enough that there was a recognizable increase in herbivory.

Exclosures could have also shown increased herbivory simply due to the absence of predation. The elimination of predators who control insect prey populations can increase herbivory by causing higher abundances of herbivores (Suwa and Louda 2012). Furthermore, it could be a combination of both the decreased risk and increased abundance that are contributing to elevated levels of herbivory.

Nutrients, however, do not seem to have as large an effect on herbivory rates. This could be in part due to the single application of fertilizer in the study, as well as due to the short time span of the study. Additionally, nitrogen may simply not be a limiting nutrient in this particular field. Since it is a successional grassland, it may merely be experiencing a flux in nitrogen (Uriarte 2000).

These cumulative trends in herbivory by insects could also be affected by a number of other factors. As they agree with the results from many forest studies, species from the surrounding forest could be having a larger effect on the plant life and ecology of the field (Koyanagi et al 2009, Blue et al 2011). Additionally, it may be late enough in succession for the field to be trending toward forest characteristics by itself (Campetella et al 2011). However, it seems more likely that a simple trophic cascade and the presence of forest species are responsible for these trends, as later successional forests are commonly nitrogen limited and there were no changes found in nutritional preferences (Uriarte 2000).

Further study of this region should include a comparison of bird predation and nutrient input on insect herbivores within the surrounding forest to confirm whether or not this field is adopting noted forest characteristics. Additionally, it would be important to compare herbivore diversity and abundance in the field and its exclosures, as well as in the forest and its potential exclosures. A more comprehensive comparison would denote with greater certainty the trends that this study found`.

Insects in forests have been shown to have the capability to completely change vegetation composition (Carson and Root 1999), but are themselves actively controlled by birds in these ecosystems at the same time (Marquis and Whelan 1994, Bruns 2009). Grasslands carry different ecological characteristics, including different nutrient, vegetation, and faunal composition, and are therefore not comparable to many ecosystems in which this particular trophic cascade has been studied (Joern 1986, Pin Koh 2008). While birds are shown to be important regulators of insects in forests, insects have been shown to both stunt the process of succession in fields (Fagan and Bishop 2000) while accelerating many other ecological processes (Schadler et al 2004) due to a slow change in both plant and insect composition (Steffan-Dewenter and Tscharntke 1997). Until this study, very few studies have sought to understand the relationship between a combination of all of these factors.

The unique characteristics of this field make it an important ecosystem in which to study these interactions. As it is a small grassland surrounded by forest and experiencing succession, it shares components of multiple ecosystems, all of which interact to create this unique habitat.

This study has shown that avian predation is an important driver of herbivory in a mixed grassland ecosystem.

Today, more and more ecosystems are experiencing changes for various ecological and anthropogenic reasons. Global bird populations are declining, further affecting these changes and putting ecosystems such as that in this study at greater risk of change. Understanding how ecosystems respond to various forms of change is important for sustaining ecosystem balance. This study has highlighted both the role of trophic interaction and nutrient composition in maintaining that balance.

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Figures and Tables

Figure 1: Schematic of UNDERC-East and the study field (Red arrow indicates North). Darker outlines represent exclosures and lighter outlines represent controls plots. Filled in plots depict where fertilizer was applied. All plots were 3 meters by 3 meters, and exclosures were approximately 36 inches tall.

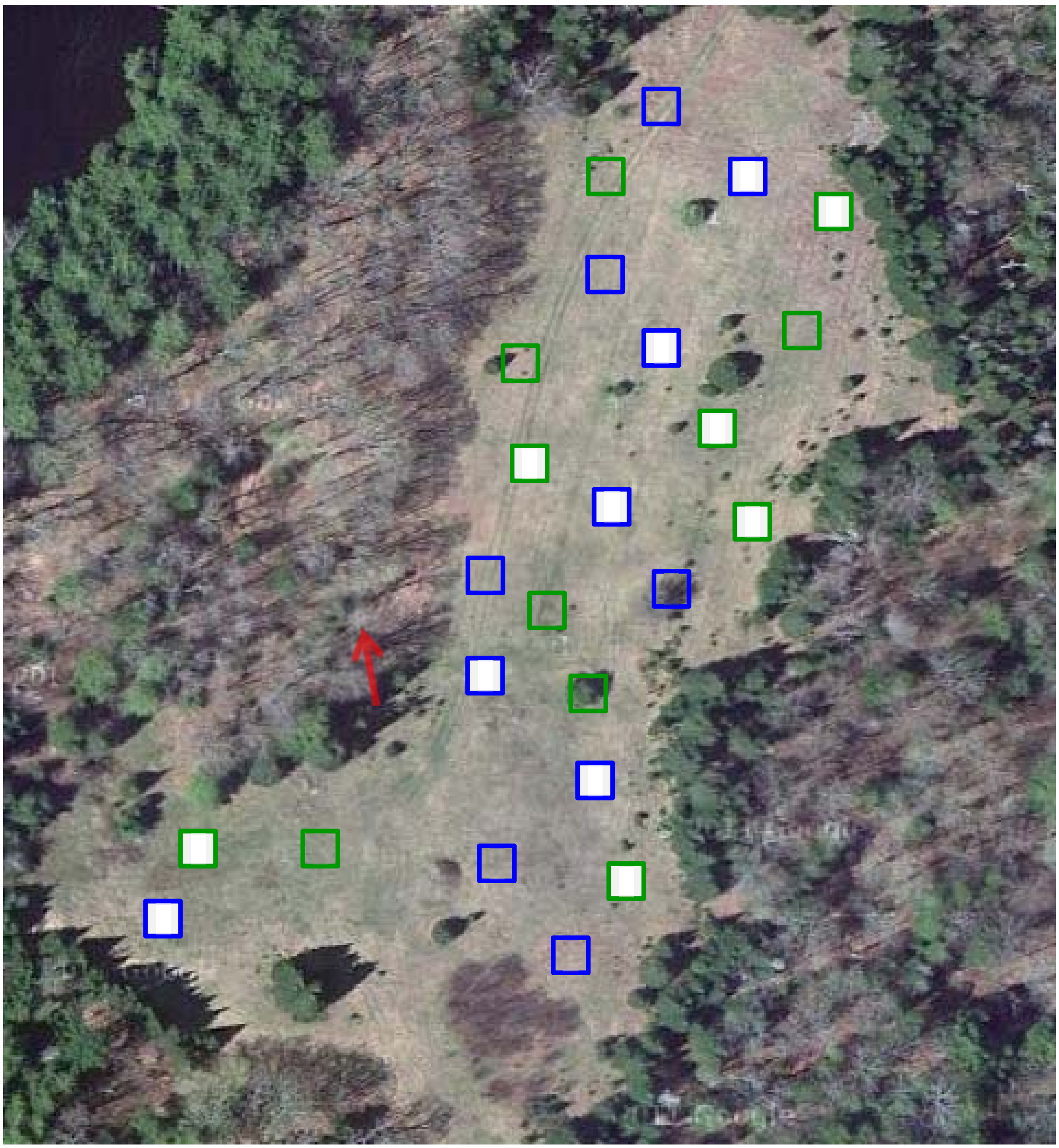

Figure 2: Exclosurers showed higher rates of herbivory in spite of the presence or absence of fertilizer (F=17.84, df= 1, p<0.001). There was no significant difference in herbivory due to fertilizer (F=0.027, df=1, p=0.41).

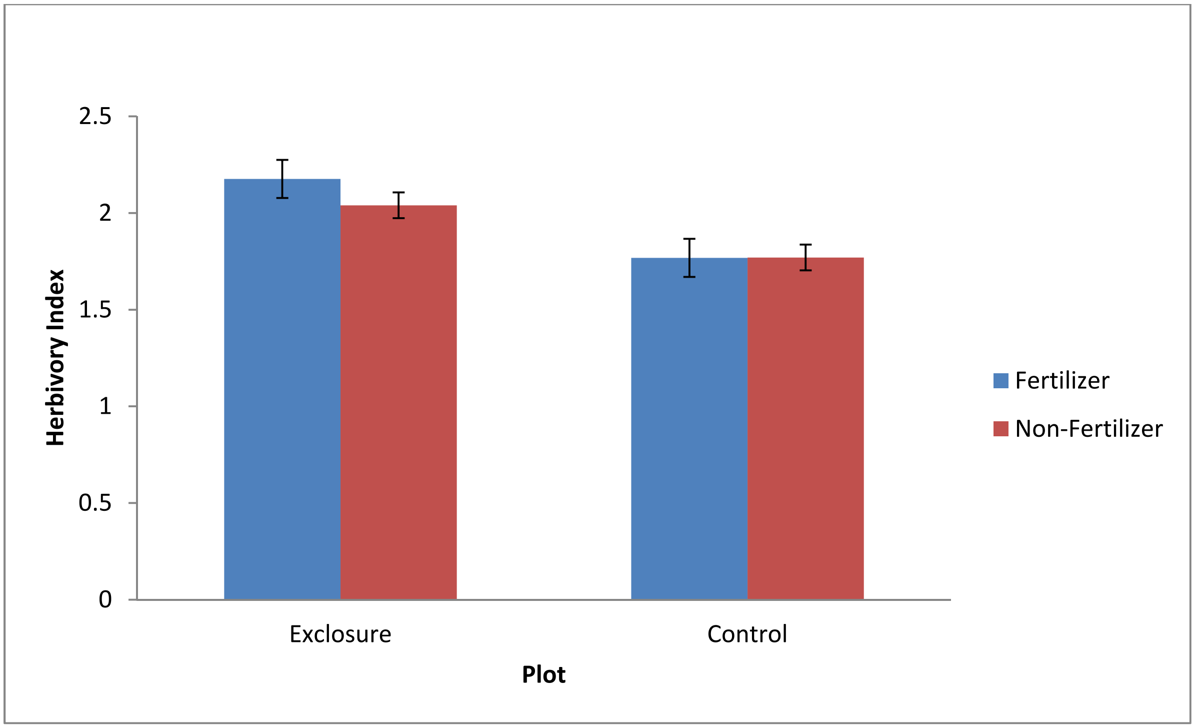

Table 1: Averages of herbivory indices between all four treatments. Exclosures showed higher rates of herbivory in spite of the presence or absence of fertilizer. There was no difference in herbivory due to fertilizer.

	Fertilizer	**Non-Fertilizer**
Exclosure	2.18	2.04
Control	1.77	1.77