

**THE EFFECTS OF HUMAN AND
ENVIRONMENTAL DISTURBANCES ON
PREDATOR-PREY INTERACTIONS**

by

Kendra Marr Lange
B.Sc. Honors, University of Alberta 2004

RESEARCH PROJECT SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF RESOURCE MANAGEMENT

In the
School of Resource and Environmental Management

Project No. 474

© Kendra Marr Lange 2009

SIMON FRASER UNIVERSITY

Summer 2009

All rights reserved. This work may not be
reproduced in whole or in part, by photocopy
or other means, without permission of the author.

APPROVAL

Name: Kendra Marr Lange

Degree: Master of Resource Management

Project Number: 474

Title of Research Project: The Effects of Human and Environmental Disturbances on Predator-Prey Interactions

Examining Committee:

Chair: **Aliaa Elkhashab**
Master of Resource Management Candidate
School of Resource and Environmental Management

Dr. Kenneth Lertzman
Senior Supervisor
Professor
School of Resource and Environmental Management
Simon Fraser University

Dr. Kristina Rothley
Supervisor
Adjunct Faculty
School of Resource and Environmental Management
Simon Fraser University

Date Defended/Approved: June 10, 2009



SIMON FRASER UNIVERSITY
LIBRARY

Declaration of Partial Copyright Licence

The author, whose copyright is declared on the title page of this work, has granted to Simon Fraser University the right to lend this thesis, project or extended essay to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users.

The author has further granted permission to Simon Fraser University to keep or make a digital copy for use in its circulating collection (currently available to the public at the "Institutional Repository" link of the SFU Library website <www.lib.sfu.ca> at: <<http://ir.lib.sfu.ca/handle/1892/112>>) and, without changing the content, to translate the thesis/project or extended essays, if technically possible, to any medium or format for the purpose of preservation of the digital work.

The author has further agreed that permission for multiple copying of this work for scholarly purposes may be granted by either the author or the Dean of Graduate Studies.

It is understood that copying or publication of this work for financial gain shall not be allowed without the author's written permission.

Permission for public performance, or limited permission for private scholarly use, of any multimedia materials forming part of this work, may have been granted by the author. This information may be found on the separately catalogued multimedia material and in the signed Partial Copyright Licence.

While licensing SFU to permit the above uses, the author retains copyright in the thesis, project or extended essays, including the right to change the work for subsequent purposes, including editing and publishing the work in whole or in part, and licensing other parties, as the author may desire.

The original Partial Copyright Licence attesting to these terms, and signed by this author, may be found in the original bound copy of this work, retained in the Simon Fraser University Archive.

Simon Fraser University Library
Burnaby, BC, Canada



SIMON FRASER UNIVERSITY
THINKING OF THE WORLD

STATEMENT OF ETHICS APPROVAL

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

(a) Human research ethics approval from the Simon Fraser University Office of Research Ethics,

or

(b) Advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University;

or has conducted the research

(c) as a co-investigator, in a research project approved in advance,

or

(d) as a member of a course approved in advance for minimal risk human research, by the Office of Research Ethics.

A copy of the approval letter has been filed at the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Bennett Library
Simon Fraser University
Burnaby, BC, Canada

ABSTRACT

Disturbance events have effects on species as well as on the interactions between species. This project includes two experiments designed to determine how human and environmental disturbances affect the interactions between species in a food web. The first experiment examined how a prey grasshopper species' mortality and food intake changed when subjected to human agitation. Grasshoppers reduced their food intake and had higher mortality rates when subjected to human disturbance, similar to how they responded to the risk of predation by spiders. The second experiment examined how the top-down control of a predator was affected when abiotic conditions were altered in a way that emulated the invasion of an exotic plant. Shading released prey from top-down control, potentially facilitating the invasion of the exotic species by removing its competition. To make effective management decisions, managers need to recognize the impact that disturbances can have on species interactions and the ecosystem.

Keywords: Density mediated interactions; Human disturbance; Invasive species; Predation Risk; Trait mediated interactions; Trophic cascade

Subject Terms: Animal behavior; Conservation biology; Effect of Human Beings on; Predation (Biology)

EXECUTIVE SUMMARY

Human induced disturbances and changes to local environmental conditions can have direct effects on species and, perhaps more importantly, the interactions between species. To determine the effect that human and environmental disturbances can have on species interactions, two experiments were conducted as a part of this project. The study system consisted of a three trophic level food chain consisting of predatory spiders (*Tibellus spp.*), prey grasshoppers (*Melanoplus sanguinipes*), and plant resources.

The purpose of the first experiment was: 1) to determine if the occurrence of human induced disturbances affect the resource use and mortality of a prey species; and 2) to compare any resource use and mortality effects caused by human disturbance with those inflicted by natural predators. I compared the mortality and resource intake of grasshoppers subjected one of four treatments: 1) a control treatment; 2) a human disturbance treatment where the researchers agitated the cage twice daily; 3) a caged non-lethal spider treatment; and 4) a lethal spider treatment. The human disturbance treatment had an effect on the grasshopper's mortality and food intake rates similar to those of the caged non-lethal spider. This suggests that even infrequent human disturbance that does not directly cause mortality can indirectly cause a change in the behaviour and mortality rates of a herbivore. These findings have important implications for the vegetative community as human induced disturbances can indirectly contribute to

the effects that herbivores have on the structure and composition of the ecosystem.

The purpose of the second experiment was to determine if shading, similar to that caused by an invasive plant species, releases prey from the top-down control of a predator in a natural field environment. I used a shading treatment to emulate the overstory conditions of a local invasive species (scotch broom (*Cytisus scoparius*)) as well as herbivore exclusion treatments to isolate the effects that the shade itself had on the vegetation. In shaded conditions there were high rates of herbivory, suggesting that there was little to no top-down control of predators on prey. Conversely, in full sun conditions, predators had a significant indirect positive effect on the plant biomass. These results reinforce the importance of species interactions on the structure and composition of the vegetative community. More importantly, the results found a previously unidentified mechanism where invasive plants, by changing abiotic conditions, can facilitate their own invasion by altering the top-down control of predators on their prey.

DEDICATION

To my husband and best friend

James

For his unwavering support and encouragement

&

To my new daughter

Avery

ACKNOWLEDGEMENTS

Thanks to Kris Rothley for all of your guidance, encouragement, and advice throughout the past three years. I appreciate all of the time and effort you put into making this project happen and I enjoyed getting to know you during the process. Also, thank you to Ken Lertzman for all of your help during the final stages of this project.

Thank you to all of my fellow REM students, professors, and support staff that made my experience at SFU memorable and enlightening.

Finally, thank you James for providing me with steady support, inspiration, encouragement, and so much more – without it I never would have started, or finished, this journey.

TABLE OF CONTENTS

Approval	ii
Abstract	iii
Executive Summary	iv
Dedication	vi
Acknowledgements	vii
Table of Contents	viii
List of Figures	ix
List of Tables	x
Glossary	xi
Chapter 1: Introduction	1
1.1 Context	1
1.2 Species Interactions	2
1.3 Study System	6
1.4 Research Objectives	9
Chapter 2: Comparing the effects of human disturbance and natural predators on a herbivore	13
2.1 Abstract	13
2.2 Introduction	14
2.3 Methods	16
2.4 Results	19
2.5 Discussion	24
Chapter 3: Can the shadow of an invasive plant mediate the top-down control of a predator?	29
3.1 Abstract	29
3.2 Introduction	30
3.3 Methods	33
3.4 Results	35
3.5 Discussion	38
Chapter 4: Discussion	42
4.1 Implications for Wildlife Management	42
4.2 Future Directions	44
4.3 Conclusion	45
Reference list	46

LIST OF FIGURES

Figure 1.1	Density mediated interactions (solid arrows) and density mediated indirect interactions (dashed arrow) in a three trophic level food chain.....	4
Figure 1.2	Trait mediated interactions (dotted line) and trait mediated indirect interactions (dashed line) in a three trophic level food chain.....	5
Figure 1.3	The three trophic level study system used consisting of a spider predator, grasshopper prey and plant resources.	7
Figure 1.4	The different types of human activity that can have effects on species interactions within food webs.....	10
Figure 2.1	Mean number of grasshoppers alive at the end of the experiment. Error bars show \pm one standard deviation.	20
Figure 2.2	Dry mass of vegetation over the course of the experiment. Error bars show \pm one standard deviation.	23
Figure 3.1	In the absence of shading, predator spiders' strong, negative top-down effect on the grasshoppers minimizes the grasshoppers' damage to the herbaceous field plants. This yields an indirect, positive effect between the spiders and the plants.....	32
Figure 3.2	In the shadow of the invading woody plant, the predator spiders' top-down effect on the grasshoppers is reduced, and grasshoppers have a significant negative impact on the herbaceous field plants. This mediation of the interaction between the spiders and the grasshoppers results in an indirect, negative effect of the woody invasive plant on the herbaceous plants with which it competes.	33
Figure 3.3	The average remaining dry weight in unshaded and shaded plots are indicated by gray diamonds and black squares, respectively, for: a) forbs and b) grasses. Error bars indicate \pm one standard deviation.	37

LIST OF TABLES

Table 2.1	Results of t-tests comparing number of grasshoppers alive at the end of the experiment and vegetation eaten. The top number in each vertical group of three numbers is the P-value of the difference between treatment means according to the least significant difference comparison. Middle number is the P-value of the two-tailed t-test comparing the means assuming unequal variances. Bottom number is the P-value of the one-tailed t-test comparing the means. Only significant ($P \leq 0.05$) and marginally significant ($P \leq 0.10$) values are shown; non-significant differences are indicated as 'NS'. If the variances between the treatments were not found to differ significantly, then middle and bottom P-value positions are shaded in light gray.....	22
-----------	---	----

GLOSSARY

DMI	Density Mediated Interactions occur when one species reduces the population density of another species through direct consumption.
DMII	Density Mediated Indirect Interactions occur when one species affects the density of another species by consuming it, causing a change in the abundance or composition of the next lower trophic level.
Food chain	The eating relationships between species that transfer energy from one organism to another.
Food web	The interlocking food chains within an ecological community.
Invasive species	Species of plants or animals not native to the region they inhabit.
TMI	Trait Mediated Interactions occur when the presence of one species causes another species to make changes in its behaviour, morphology or life history traits.
TMII	Trait Mediated Indirect Interactions occur when one species invokes a behavioural response from another species that is significant enough to affect the next lower trophic level.
Trophic cascade	Occurs when predators in a food chain suppress the abundance of their prey, thereby releasing the next lower trophic level from predation.
Trophic level	The position that an organism occupies in a food chain, such as a primary producer, herbivore, carnivore, etc.

CHAPTER 1: INTRODUCTION

1.1 Context

There is undeniable evidence that the environment is becoming more and more disturbed by human activity, whether it be from direct human development (He 2009), habitat fragmentation (Songer et al. 2009), or the introduction of invasive species (Jarnevich and Stohlgren 2009, Leung 2009). Extensive research has been, and is being, done that examines how species are responding to these environmental changes (Xu et al. 2009, Ritchie et al. 2009, Gonzalez-Varo et al. 2009, Davis et al. 2008) and researchers are seeking solutions for how to mitigate or reduce the impact that humans are having on individual species and ecosystems (Lindenmayer 2009). Though this research is critical, studies that focus on how changing environmental conditions affect the interactions between species are also important as ecosystems are composed of food webs comprised of interacting species. By understanding how the strength of species interactions change with biotic or abiotic context, community ecology can become more quantitative and predictive (Agrawal et al. 2007). Because behavioural ecology can inform community ecology (Dill et al. 2003), it is important that we focus research on how species interactions respond to

environmental perturbations so that we can better predict, mitigate, and manage the effect of current and future environmental disturbance.

1.2 Species Interactions

There are a number of different types of species interactions, including competition, mutualism, predation, etc. When studying population and community ecology, predation is especially interesting because predators can have a tremendous influence on community structure and dynamics (Schmitz et al. 1997). As the density of prey species changes, the abundance and composition of the next lower trophic level are altered, potentially leading to significant and widespread ecological effects. The indirect effects that predators can have on their prey's food resources has been given the term 'trophic cascade' (Paine 1980), which can be thought of in a three trophic level food chain as the indirect effects of carnivores on plants, mediated by herbivores (Schmitz et al. 2004).

A classic example of a trophic cascade is the sea otters, sea urchin, and kelp food chain in the Pacific Ocean. Estes and Palmisano (1974) found that when sea otters are present the population of their food source, sea urchins, remains low. The low numbers of sea urchins thereby releases their food source, kelp, from the effects of herbivory. In areas where sea otters have been hunted to extinction, the sea urchin population has increased, decimating the kelp in the area. Therefore, the presence of sea otters has a direct negative effect on the sea urchins and an indirect positive effect on the kelp. The sea otter, sea urchin, and kelp example illustrates a system where there is top-down control because

the ecosystem is controlled by the abundance of predators, not by the productivity of the kelp.

A terrestrial example of a trophic cascade is the wolf, elk, and aspen food chain in Yellowstone National Park. Since the extirpation of the wolves in the 1920's, the elk population has increased while aspen recruitment has declined (Ripple and Larson 2000). However, after wolves were reintroduced to the Park in 1995, the first documented growth of aspen in the past 50 years was observed, especially in areas where there was high wolf predation risk (Ripple and Beschta 2007).

Two types of predator-prey interactions can cause trophic cascades. Most commonly, researchers and managers consider predator-prey interactions in terms of consumption: the predators capturing, killing, and consuming their prey. These interactions are termed density mediated interactions (DMI) because when predators consume their prey, they have a negative impact by reducing overall density of the prey (Figure 1.1). Simultaneously, prey species have a positive direct effect on the predators as the predators' growth and reproductive capabilities increase as they consume more prey (Preisser et al. 2005). In turn, prey species have a direct negative effect on their vegetative food sources by consuming them, while the amount of vegetation in the system has a positive impact on the prey (Figure 1.1).

Due to the negative effect that predators have on their prey, a positive indirect effect occurs between the predators and plant resources. As the number of individual prey decrease, plant resources are released from the pressures of

herbivory. The positive indirect effects that occur between the predators and the plant resources are termed density mediated indirect interactions (DMII) (Abrams 1995) (Figure 1.1).

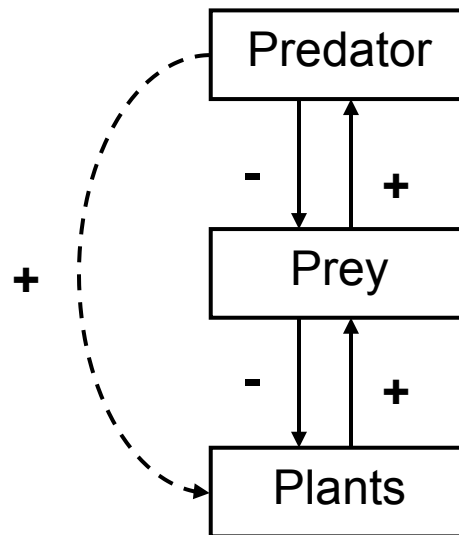


Figure 1.1 Density mediated interactions (solid arrows) and density mediated indirect interactions (dashed arrow) in a three trophic level food chain.

The second way that predators can interact with their prey to cause trophic cascades is termed trait mediated interactions (TMI). A TMI occurs when predators have ‘non-lethal’ or ‘non-consumptive’ effects on their prey. When in the presence of a predator, prey may alter their behaviour, morphology, or life history traits (Werner and Peacor 2003), potentially causing a reduction in the prey’s foraging effort (Morrison 1999), energy income (Downes 2001) and even reproductive success (Barry 1994, Dunn et al. 2008). Similar to a DMII, when

predators have a 'non-lethal' effect on their prey, such as causing a change in the prey's foraging behaviour, it can lead to an indirect interaction between the predators and the plant resources (Figure 1.2). These indirect interactions are called trait mediated indirect interactions (TMII) (Abrams 1995) because they are caused by a change in the prey's traits, rather than prey density. Though it is convenient to think of TMI and DMI as occurring independently, it is more realistic to assume that they are occurring simultaneously. For example, when a predator catches and consumes an individual prey species (a DMI), other prey may witness the attack and therefore increase the magnitude of their predator avoidance behaviour (a TMI).

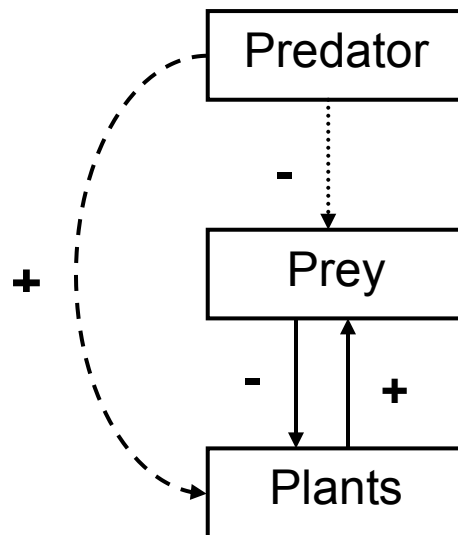


Figure 1.2 Trait mediated interactions (dotted line) and trait mediated indirect interactions (dashed line) in a three trophic level food chain.

When comparing the relative importance of DMII and TMII, research suggests that indirect effects resulting from anti-predator behaviour can be similar in form and strength to the effects caused by direct predation events (Schmitz et al. 1997, Trussell et al. 2006, Preisser et al. 2005). A potential explanation for why TMII can have such widespread effects is that predators can influence the behaviour of many individuals at the same time while each predation event only affects a single herbivore (Schmitz et al. 1997). Similarly, TMII may contribute more to the indirect effect of predators because non-lethal predator effects are immediate and can occur over the entire lifetime of the prey (Peacor and Werner 2001). Both DMII and TMII are important and can have substantial effects on the composition and structure of the ecosystem; therefore, it is critical that both mechanisms are studied when researching predator-prey dynamics and their impacts on ecosystems.

1.3 Study System

The three trophic level study system used for the two experiments outlined in this study is comprised of predatory spiders (*Tibellus spp.*), herbivorous grasshoppers (*Melanoplus sanguinipes*) and the grasshopper's vegetative food resources, primarily consisting of grass (blue joint (*Calamagrostis canadensis*) and smooth meadow grass (*Poa pratensis*)), and forb species (primarily dandelion (*Taraxacum officinale*) and white clover (*Trifolium repens*)) (Figure 1.3).

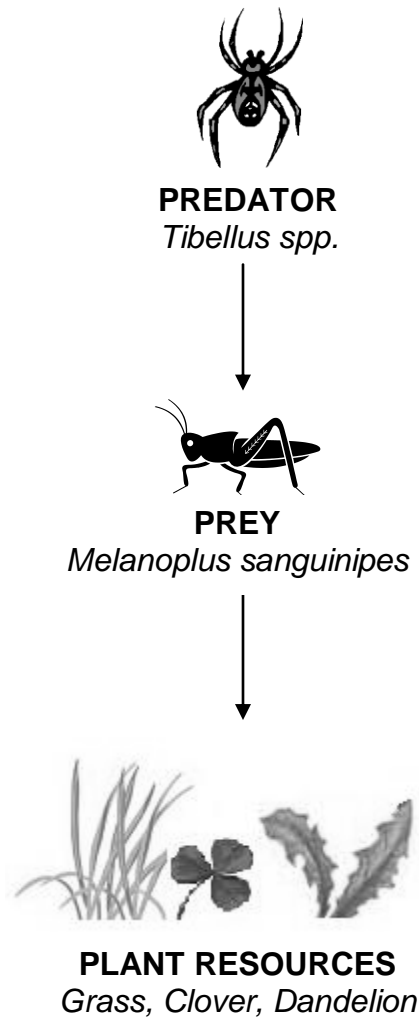


Figure 1.3 The three trophic level study system used consisting of a spider predator, grasshopper prey and plant resources.

I used the spider-grasshopper-plant study system for a number of reasons. When studying trophic interactions, large scale, fully replicated experiments with significant statistical power are usually very difficult and

expensive to conduct (Schmitz 2005). Because of the nature and small scale of the study system I used, I was able to test numerous experimental variables simultaneously, while still performing enough replications to provide meaningful statistical results. When studying predator-prey dynamics and their implications for ecological systems, managers tend to desire research done on large scale landscapes, as this tends to be the scale that most management decisions are made. However, Schmitz (2005) argues that meadow and boreal systems can be viewed as systems of interacting carnivores, herbivores, and plants that are essentially the same from a functional standpoint. Therefore, small-scale experiments are useful in that they can test the fundamental principles of predator-prey interactions and then be applied to other functionally similar ecological systems.

Another reason I used this study system is that there have been numerous experiments performed on this, or very similar, study systems, providing ample background information on the trophic dynamics and behavioural responses of these species. Rothley et al. (1997) demonstrated that grasshoppers make a trade off between energy intake and time spent being vigilant in response to predation risk. Schmitz et al. (1997) measured the mortality and resource use of grasshoppers in the presence of predatory spiders and 'risk spiders'. In the Schmitz et al. (1997) experiment the 'risk spiders' were spiders that had their mouthparts glued shut so that they could not consume the grasshoppers. They found that the mortality rates of the grasshoppers increased when in the presence of the predatory spiders (a DMI) the same amount as when they were

in the presence of the 'risk spiders' (a TMI). They also observed that both the predatory and 'risk' spider treatment had a positive effect on the grass, thus demonstrating the presence of a trophic cascade.

Schmitz et al. (2001) studied how predators within the same guild can have different trophic level effects. For example, they found that predators who actively hunted their prey had only density mediated indirect effects on plants, while spiders that used a sit-and-wait hunting approach caused a change in the grasshoppers' foraging behaviour leading to trait mediated indirect effects on the plants.

Rothley and Dutton (2006) measured the effects of altered environmental conditions on predator-prey interactions. They found that, in unshaded conditions, grasshoppers responded to the presence of spiders by decreasing their energy intake, reducing time spent feeding, and shifting their diet (consuming more grass), all of which may increase mortality leading to a trophic cascade. However, in shaded conditions, the grasshoppers did not respond to the presence of spiders and no trophic cascade was observed.

1.4 Research Objectives

Different types of human activity (Figure 1.4) can disturb food webs and their associated species interactions (Faeth 2005). Human activity can act as a substitute for predators in an ecological system and can affect the density of prey species in the same way that predators do (Frid and Dill 2002). For example, like

DMI between predators and prey, hunting can cause a direct reduction in the number of animals in a population (Torres-Porras et al. 2009). Similarly, loss of natural habitat due to development, climate change, invasive species or fragmentation could potentially reduce the overall fitness and reproductive success of prey species in a way that alters the abundance and composition of the vegetative community (a DMII) (Schmitz and Suttle 2001).

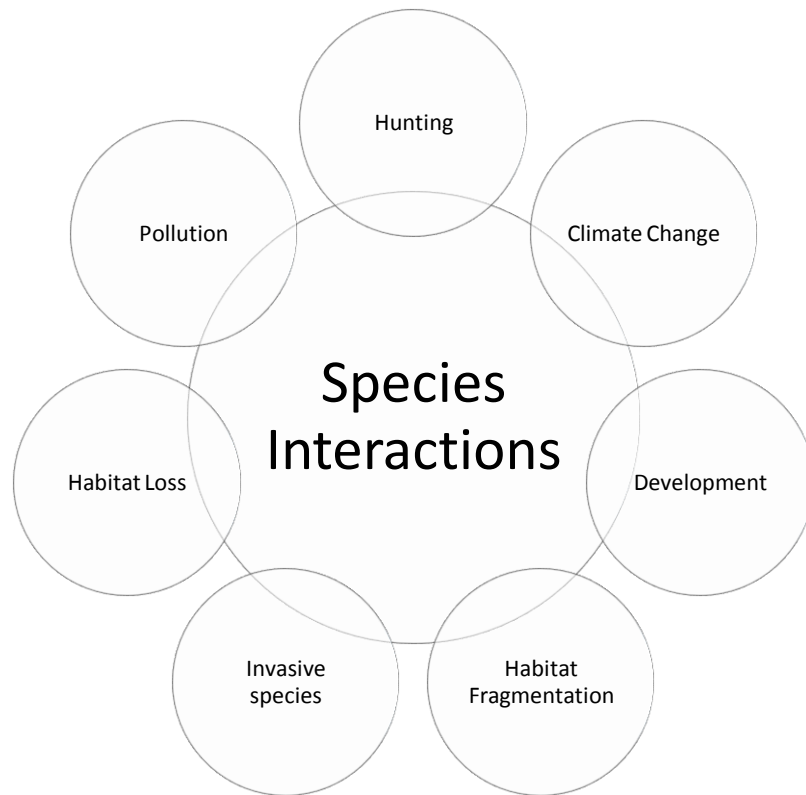


Figure 1.4 The different types of human activity that can have effects on species interactions within food webs.

Like predators, humans can also have a number of non-lethal effects on prey. The risk disturbance hypothesis suggests that prey are likely to follow the same economical principles when disturbed by humans as they do when they encounter predators (Frid and Dill 2002). Therefore, human activities such as traffic or tourism can produce light or noise pollution that can cause prey to trade fitness maximizing activities, such as foraging or searching for mates, for vigilance behaviour, just as they would in the presence of a predator (a TMI) (Frid and Dill 2002). As a result, when designing and constructing protected areas, the implications of human activities require consideration. Even if human use is restricted within protected areas species may still be vulnerable to outside human activity that can permeate the protected area boundaries.

To examine the effect that human activity can have on predator-prey interactions I conducted the experiment outlined in Chapter 2. The purpose of this experiment was to compare herbivore behaviour and mortality responses to both human disturbance and natural predators. The two specific questions that I addressed were: 1) does human disturbance affect resource use and mortality of prey grasshoppers; and 2) if so, how does this response compare to resource use and mortality effects caused by both lethal and non-lethal predators?

Similarly, alterations to the abiotic conditions of ecosystems can have an effect on predator-prey interactions (Rothley and Dutton 2006). Chapter 3 presents a field experiment where the abiotic conditions (temperature, wind, light) were altered in a way that emulated the overstory cover of an introduced invasive species (scotch broom, *Cytisus scoparius*). The goal of this experiment was to

determine if shading conditions (decreased light and temperature) release prey species from the top-down control of a predator in a natural field environment.

The purpose of conducting the experiments outlined in chapters 2 and 3 was to further the understanding of species interactions to illustrate the importance of TMI and TMII, and to look at how species interactions are effected by environmental perturbations. As human disturbance of natural ecosystems continues to increase, so will the need to more fully understand these mechanisms. Chapter 4 will provide implications for wildlife management and future directions for research on these topics.

CHAPTER 2: COMPARING THE EFFECTS OF HUMAN DISTURBANCE AND NATURAL PREDATORS ON A HERBIVORE¹

2.1 Abstract

Growing empirical evidence suggests that human induced disturbance can elicit the adaptive, anti-predator behaviours that animals use in response to predation risk. I conducted an experiment with predator spiders, prey grasshoppers, and plant resources to directly compare the effects of human disturbances with those generated by a natural predator. I compared the diet, food intake, and mortality of grasshoppers in the absence of predators and disturbance, in the presence of caged predators, in the presence of free-roaming predators, and subjected to a short duration of agitation by the human experimenters twice daily. The effect of the human disturbance on the grasshoppers' mortality, food intake, and diet was nearly identical to that of the caged spider. The free-ranging spider caused similar levels of mortality but a stronger reduction in food intake. My results suggest that infrequent human disturbance can change herbivore behaviour and mortality, even if it does not involve direct mortality. Given the strong effect that herbivores can exert on the

¹ The experiment described in this chapter was designed, conducted, and written in partnership with K.D. Rothley.

structure and function of vegetative communities, human disturbance may indirectly but substantially contribute to these effects.

2.2 Introduction

Numerous studies have documented the negative impacts of humans on animal populations, such as the indirect density effects caused by habitat alteration, loss, or fragmentation (Yasue and Dearden 2006) and climate change (Stirling and Parkinson 2006), or the direct density effects of hunting or the interruption of reproductive activities (Beale and Monaghan 2004, Moore and Seigel 2006). Humans can also cause direct, non-lethal effects on animals via noise, light, vehicular or pedestrian traffic, or direct physical interactions (Rode et al. 2006). In some instances, these stimuli generate a non-specific startle response, a physiological change (Tarlow and Blumstein 2007), or confound the animals' normal behaviour, such as when artificial lighting confounds the orientation of sea turtle hatchlings (Tuxbury and Salmon 2005).

Behavioural ecologists have proposed that anthropogenic stimuli can also elicit the adaptive, anti-predator behaviours that animals use in response to predation risk (Gavin and Komers 2006). Specifically, human disturbance can cause prey animals to trade fitness maximizing activities, such as foraging or mate searching, for risk minimizing behaviour such as vigilance, just as natural predators do (Lima and Dill 1990, Abrams 1993, Frid and Dill 2002). Prey will also utilize sub-optimal food or habitat to minimize their risk (Brown and Kotler 2004).

There are several reasons why the potential for humans to induce anti-predator behaviour in prey is an important area of research. First, growing empirical evidence supports the theory that anti-predator behaviour can have significant consequences for populations, communities, and ecosystems (Křivan and Schmitz 2004, Preisser et al. 2005). Hence, human disturbances that generate anti-predator behaviour also have the potential to generate these consequences. Second, anthropogenic disturbances, such as the sounds from engines (airplane, automobile, or boat) and firearms, can travel over long distances and permeate even remote areas and disrupt animal behaviour (Foote et al. 2004). Therefore, the physical or cadastral bounds of protected areas are vulnerable to these influences. Third, with the growing human population and concomitant expanding footprint of development and resource extraction, human disturbance will only become more prevalent (Vitousek et al. 1997). Fourth, the level and temporal pattern of human disturbance can alter predator behaviour (Hebblewhite et al. 2005) or prey's normal risk response (Fernández-Juricic et al. 2003, Webb and Blumstein 2005). Hence, prey could become more vulnerable to potential harm (Semeniuk et al. 2007). Finally, the wealth of existing information regarding predator-prey interactions may help to inform both our predictions of animals' responses to future human disturbance and management strategies aiming to reduce the impacts of humans on wildlife.

I performed an experiment that compared the effects of human disturbance and both lethal and non-lethal (caged) natural predators on a herbivore's behaviour and mortality in a predator-prey-resource system. Many

studies have documented how human induced disturbances have yielded an anti-risk response in prey (e.g., Gavin and Komers 2006, Rothley 2002). However, few studies have directly compared the responses of prey to a controlled human disturbance versus natural predators (Parsons and Eggleston 2006). My first goal was to determine if human disturbance would affect the resource (plant) use and mortality of a prey grasshopper (*Melanoplus sanguinipes*). The second goal was to compare any resource use and mortality effects of human disturbances with those inflicted via trait and density effects of predatory crab spiders (*Tibellus* sp.) on the grasshopper.

2.3 Methods

I conducted this study in a 1.8m by 3m greenhouse in July 2007 at Simon Fraser University located on Burnaby Mountain in Burnaby, British Columbia. All animals used in this experiment were collected locally. Thirty-two cages were assigned to one of four treatments: 1) control: no human disturbance or spider predator, 2) human disturbance, 3) nonlethal crab spider, and 4) lethal crab spider. The cages were arranged in eight blocks (with the treatments randomly assigned within the blocks) to accommodate any temperature gradient across the greenhouse that may have affected the plants or animals. I chose this number of blocks based on the amount of time required for set-up (I wanted the start time for all cages to be within a couple hours of each other) and the variability in grasshopper foraging rates displayed in previous experiments with these animals. Two additional treatments with a lethal and non-lethal wolf spider

(Family Lycosidae) were also attempted. However, all of these spiders died and I excluded the results from these cages from the analysis.

The circular cages were 38cm tall with a diameter of 12.7cm and were constructed from black Teflon® insect netting and plastic flowerpots. For each cage, one dandelion leaf (*Taraxacum officinale*), two clover leaves (*Trifolium repens*) and three blades of grass (*Calamagrostis canadensis*) were placed in separate vials of water to minimize desiccation. The plant material largely, but not entirely, blocked the grasshoppers' access to the water. The vials were then set in a glass at the bottom of the cage (the physical arrangement of the resources was the same for all treatments) with the vegetation sticking out over the rim of the glass. All vegetation was traced by hand onto paper prior to the start of the experiment. I then added four second or third instar grasshoppers to each cage. Previous trials showed that grasshoppers of these sizes can be readily captured and eaten by the spiders (Rothley and Dutton 2006).

For cages assigned to the lethal crab spider treatment, I added one spider to the cage along with the four grasshoppers and it was free to move throughout the cage. For cages assigned to the nonlethal crab spider treatment, one spider and one grasshopper (in addition to the four grasshoppers in the main area of the cage) were confined in an aluminum screen box (13 x 9 x 4cm) placed within the main cage near the top. The grasshopper was included with the spider to minimize the likelihood that the spider would starve to death during the experiment and to maximize the similarity between the spider behaviour in the

non-lethal and lethal treatments where grasshoppers were likely to witness attacks.

Cages that were assigned to the human disturbance treatment were forcefully tapped at their bases and along the mesh top twice daily for 30 consecutive seconds. I chose this form of human disturbance to mimic the physical agitation I created when walking through my field site (where I collected the animals for this experiment). In response to this human agitation in the grasshoppers natural habitat, I observed the grasshoppers “freeze”, hide (move behind vegetation), or jump, similar to the way the grasshoppers in the greenhouse reacted to the cage tapping.

After five days, the surviving animals were counted and released into the fields where they were caught. The remaining, uneaten vegetation was re-traced to measure the area of plant material eaten by the grasshoppers. The plant area consumed was converted into dry-weight equivalents using area to dry-weight ratios, and then to wet-weight equivalents for the percent grass calculations using wet-mass/dry-mass ratios.

I used an ANCOVA analysis including the treatments and the relative distance from the green house door as independent variables to test the effects of these factors on the number of grasshoppers alive at the end of the experiment and the vegetation eaten. If I found that the relative distance from the green house door was not significant, I used an ANOVA to test for a treatment effect. The differences between treatment means were then compared against

the least significant difference (LSD; calculated from a multiple t-test that uses a pooled estimate of variance from all treatments).

I tested the homogeneity of variances between treatments of the number of grasshoppers alive at the end of the experiment and the vegetation eaten using the Levene's F-test. If the variances were found to differ significantly, I used the Welsh ANOVA (in addition to the standard ANOVA) to test for the significance of the treatments. I then tested the mean of each pair of treatments (in addition to the LSD comparison) individually using two-tailed (most comparable to the result of the LSD test) and one-tailed t-tests assuming unequal variances. In order to be able to compare my results with previous studies, the vegetation eaten data was analyzed using the categories grass (grass only) and forbs (dandelion and clover).

2.4 Results

The relative distance from the green house door had no significant effect on the number of grasshoppers alive at the end of the experiment ($F_{4,27}=3.07$, $P_{\text{ANCOVA}}=0.03$, $P_{\text{block}}=0.48$, $P_{\text{treatment}}=0.02$), but the treatment effect was significant ($F_{3,28}=3.99$, $P_{\text{ANOVA}}=0.02$). No significant difference between the treatment variances was detected ($P_{\text{Levene test}}=0.40$). The lowest mean number of grasshoppers alive at the end of the experiment was in the lethal spider cages (Fig. 2.1). On average, the control cages had significantly more grasshoppers

alive at the end of the experiment than the human disturbance cages, the non-lethal predator cages, and the lethal predator cages (Table 2.1a; Fig. 2.1).

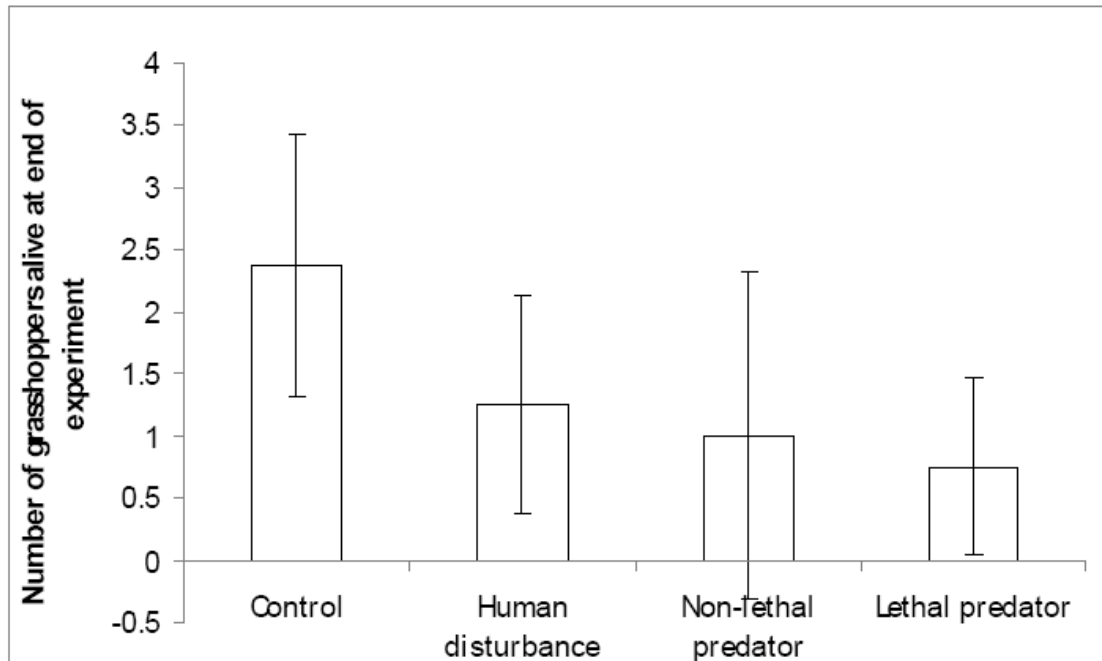


Figure 2.1 Mean number of grasshoppers alive at the end of the experiment. Error bars show \pm one standard deviation.

The relative distance from the green house door had no significant effect on the total amount of vegetation eaten ($F_{4,27}=2.26$, $P_{\text{ANCOVA}}=0.09$, $P_{\text{block}}=0.49$, $P_{\text{treatment}}=0.06$), but the treatment effect was significant ($F_{3,28}=2.90$, $P_{\text{ANOVA}}=0.05$). I found the variance between treatment groups to be unequal ($P_{\text{Levene test}}<0.01$) but the Welsh ANOVA also indicated a significant treatment effect ($F_{3,13.10}=8.51$, $P<0.01$). Grasshoppers in the lethal crab spider cages ate the lowest average total vegetation (Fig. 2.2). Total vegetation eaten in the lethal crab spider cages

was significantly lower than in the control cages and the human disturbance cages, and marginally different from the non-lethal predator cages (Table 2.1b). The percent of the grasshoppers' diet comprised of grass, on average, was 6.9% in the control cages, 7.2% in the lethal crab spider cages, 13.3% in the non-lethal crab spider cages, and 22.8% in the human disturbance cages.

The relative distance from the green house door had no significant effect on the amount of forbs eaten ($F_{4,27}=2.25$, $P_{\text{ANCOVA}}=0.09$, $P_{\text{block}}=0.88$, $P_{\text{treatment}}=0.05$), but the treatment effect was significant ($F_{3,28}=3.10$, $P_{\text{ANOVA}}=0.04$). The variance between treatment groups was found to be unequal ($P_{\text{Levene test}}<0.01$) but the Welsh ANOVA also indicated a significant treatment effect ($F_{3,13.50}=8.87$, $P<0.01$). Grasshoppers in the lethal crab spider cages ate the lowest average forbs (Fig. 2.2). Forbs eaten in the lethal crab spider cages were significantly lower than in the control cages and the human disturbance cages, and marginally different from the non-lethal predator cages (Table 2.1c). Forbs eaten in the human disturbance cages were significantly lower than in the control cages.

Neither the relative distance from the green house door nor the treatment had a significant effect on the amount of grass eaten ($F_{4,27}=2.93$, $P_{\text{ANCOVA}}=0.04$, $P_{\text{block}}=0.06$, $P_{\text{treatment}}=0.07$) if the variances between the treatments were assumed to be homogenous. However, I found the variance between the treatment groups to be unequal ($P_{\text{Levene test}}=0.05$) and the Welsh ANOVA indicated a significant treatment effect ($F_{3,12.68}=4.04$, $P=0.03$). Grasshoppers in the lethal crab spider cages ate the lowest average grass (Fig. 2.2). Grass eaten

Table 2.1 Results of t-tests comparing number of grasshoppers alive at the end of the experiment and vegetation eaten. The top number in each vertical group of three numbers is the P-value of the difference between treatment means according to the least significant difference comparison. Middle number is the P-value of the two-tailed t-test comparing the means assuming unequal variances. Bottom number is the P-value of the one-tailed t-test comparing the means. Only significant ($P \leq 0.05$) and marginally significant ($P \leq 0.10$) values are shown; non-significant differences are indicated as 'NS'. If the variances between the treatments were not found to differ significantly, then middle and bottom P-value positions are shaded in light gray.

	Human disturbance	Non-lethal spider	Lethal spider
a. Total grasshoppers alive at the end of the experiment			
Control	0.04	0.01	<0.01
Human disturbance		NS	NS
Non-lethal spider			NS
b. Total vegetation eaten [g-dry]			
Control	NS	NS	<0.01
Human disturbance		NS	0.05
Non-lethal spider		NS	0.02
		NS	0.01
			0.09
			NS
			0.07
c. Forbs eaten [g-dry]			
Control	NS	NS	<0.01
Human disturbance	0.09	NS	<0.01
Non-lethal spider	0.04	NS	<0.01
		NS	NS
		NS	0.03
		NS	0.02
			NS
			NS
			0.10
D. Grass eaten [g-dry]			
Control	NS	NS	NS
Human disturbance	NS	NS	NS
Non-lethal spider	0.10	NS	0.05
		NS	0.01
		NS	0.02
		NS	0.01
			NS
			NS
			0.10

in the lethal crab spider cages was significantly lower than in the control cages and the human disturbance cages, and marginally less than in the non-lethal predator cages (Table 2.1d). Grass eaten in the control cages was marginally lower than in the human disturbance cages.

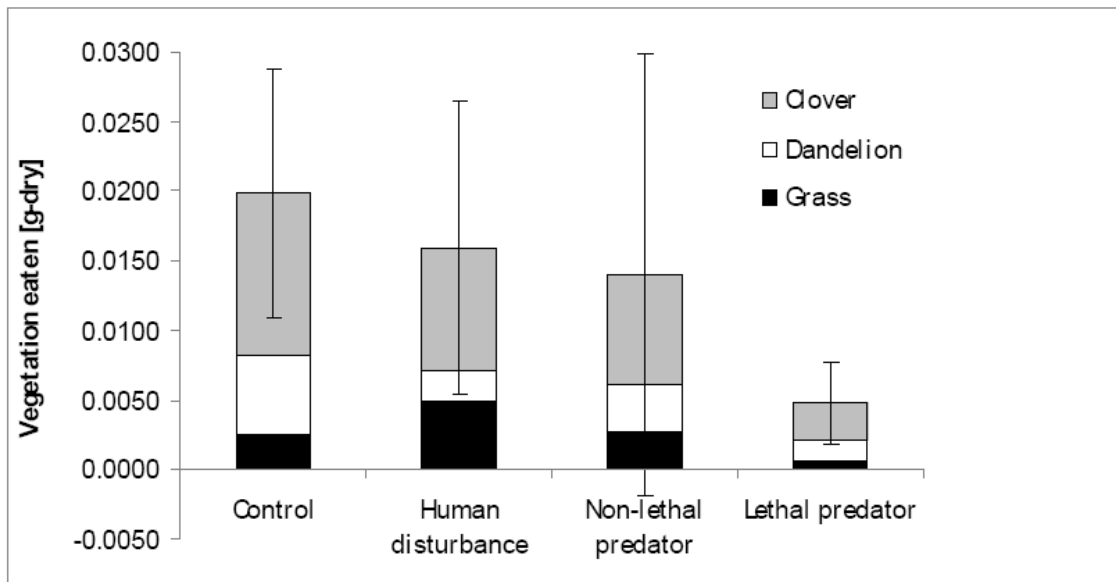


Figure 2.2 Dry mass of vegetation over the course of the experiment. Error bars show \pm one standard deviation.

2.5 Discussion

The human disturbance treatment affected the grasshoppers with respect to their mortality, diet composition, and the quantity of food eaten as compared to grasshoppers in the control cages. Grasshopper mortality was significantly higher in the human disturbance cages compared to the control (Table 2.1a; Fig. 2.1). This mortality was the result of the grasshoppers' behavioural responses to the treatment as none were, to my knowledge, directly killed or harmed during the application of the disturbance. Part of the explanation for the elevated mortality may have been the associated diet shift. Relative abundance of grass in the grasshoppers' diet in the human disturbance cages was over three times larger than in the control cages. Elevated diet ratios of grasses to forbs have been shown to have fatal consequences for the *M. Sanguinipes* grasshopper and other closely related species (see Rothley and Dutton 2006). Starvation may have also contributed to the elevated mortality. Forbs eaten in the human disturbance cages were significantly lower than in the control cages, although grass eaten in the human disturbance cages was marginally significantly higher than in the control cages (Tables 2.1c and 2.1d).

In comparison to the natural predators, the character and intensity of the consequences of the human disturbance were nearly identical to those of the non-lethal spiders. There was no significant difference between these treatments on the mortality of the grasshoppers, and both treatments resulted in significantly more dead grasshoppers than in the control (Table 2.1a). There was no difference in total vegetation or grass eaten by grasshoppers in the human

disturbance and non-lethal spider treatments, or between either of these treatments and the control (Tables 2.1b and 2.1d). There was no difference in the forbs eaten by grasshoppers in the human disturbance cages and the non-lethal spider cages, although forbs eaten in the human disturbance cages were significantly lower than in the control cages (Table 2.1c). Both treatments also resulted in an elevated ratio of grasses to forbs in the grasshoppers' diet as compared to the control cages.

In contrast, the effects of a lethal predator were similar to, but could be distinguished from, those of the human disturbance. While there was no difference in grasshopper mortality between the lethal grasshopper and human disturbance cages (Table 2.1a), total vegetation eaten, forbs eaten, and grass eaten were significantly lower in the lethal spider cages (Tables 2.1b, 2.1c, and 2.1d). Also, the increase in the percent of the diet comprised of grass for the lethal spider treatment was relatively minor compared to the increase caused by the human disturbance treatment.

Based on the similarities between the outcomes of the treatments, it is reasonable to conclude that the human disturbance invoked behaviours similar to the anti-predator behaviour the grasshoppers use in response to natural predation risk. An obvious question is "why?", given that I did not use artificial spiders as part of the disturbance and the cage tapping in no way resembled any conditions that might occur when a predator attack occurs. One reason could be that the immediate outcome of the treatments on the grasshoppers was similar. I observed that in response to the human disturbance treatment, grasshoppers

either froze, hid, or jumped, and presumably this behavioural repertoire is the same in response to natural predators. I could not directly watch this without potentially compromising the treatments, but I have been experimenting with video recording equipment as a means to indirectly collect this data.

A second question is why the grasshoppers' response to human disturbance looked so similar to their response to non-lethal spiders but dissimilar, with respect to food intake quantities, to lethal spiders. One explanation is that while the human disturbance and non-lethal spiders can only cause direct behavioural effects, the lethal spiders also generate a density effect potentially making them "scarier" to surviving prey (note that total vegetation eaten in the lethal spider cages was significantly and marginally significantly lower than in the human disturbance and non-lethal spider cages, respectively, even though there was no difference in the number of grasshoppers alive at the end of the experiment in these treatments). Another explanation is the possible varying rapidity with which the treatments resulted in grasshopper mortality. To avoid confounding the human disturbance treatment, I only counted the number of grasshoppers alive at the beginning and end of the experiment. Perhaps the deaths in the lethal spider cages occurred sooner and therefore the effect on the plants was more exaggerated.

The results of the greenhouse experiment described here have potentially important implications for the interaction of humans and the environment. According to my results, it would be reasonable to hypothesize that human disturbance could result in trait mediated grasshopper mortality and changes in

grasshopper diet and food quantity intake that would eventually lead to a shift in vegetation density (the trophic cascade pattern generated by top-down control) and composition, assuming that the disturbance effects were not compensatory to those of natural predators or if natural predators were absent. Another possibility is that the human disturbance could exaggerate the consequences of a natural predator's presence on the prey's mortality (Parsons and Eggleston 2006) or behaviours such as vigilance (Peters and Otis 2005). To generate community changes, the human disturbance need not resemble a natural predator and its duration could be relatively brief (note that the human disturbance treatment was only applied twice daily for 30 consecutive seconds). Additionally, if the increase in grass in the grasshoppers' diet is associated with increased mortality, then human disturbance could have stronger effects on the grasshoppers than the natural predators over time.

Through direct interactions with plant resources, herbivores may single-handedly shape the plant community structure and function (Schmitz 2005). If, as I found in the experiment described here, even non-lethal and infrequent human disturbance can change herbivore behaviour and mortality, then it would be reasonable to suppose that human disturbance could have profound effects on communities even if that disturbance, such as the substantial auditory and olfactory cues generated by human activity such as development, transportation, and recreation, does not involve direct mortality (Tarlow and Blumstein 2007). An interesting follow up to the experiments described here might be to explore whether human disturbance similar in nature to the one employed from the

greenhouse setting would cause similar mortality in a natural field setting, where variable local conditions such as noise, avian predators, or wind, for example, might dilute its effect.

CHAPTER 3: CAN THE SHADOW OF AN INVASIVE PLANT MEDIATE THE TOP-DOWN CONTROL OF A PREDATOR?²

3.1 Abstract

Changes in local environmental conditions can directly impact species as well as influence the interactions between species. I was interested in how shadows cast by an invading woody plant might influence a spider's top-down control on grasshoppers, and what the consequences might be for the vegetative community. The treatments included both shading similar to that created by the invasive plant and herbivory exclusion to partition out the direct effects of the light levels from the impacts of herbivory on the plants. I found that in shadows little top-down control was detected, as evidenced by relatively high herbivory levels, while in full sun predators had a significant indirect positive effect on plant biomass. Had I not controlled for grasshopper herbivory, the association between shade levels and vegetation density would have been misinterpreted as a direct effect of light on the plants. These results demonstrate the important role that species interactions play in the response of communities to perturbations, and

² The experiment described in this chapter was designed, conducted, and written in partnership with K.D. Rothley.

suggest a previously unknown mechanism by which an invasive plant, through the alteration of top-down control, may facilitate its own invasion.

3.2 Introduction

Top-down control by predators can have powerful effects on the composition and dynamics of communities (Schmitz and Suttle 2001; Knight et al. 2005; Sergio et al. 2005; Tylianakis et al. 2007), and the significant consequences of the loss of top-down control have been demonstrated in a wide range of terrestrial and marine ecosystems (Moksnes et al. 2008, Paine 1980, Ripple and Breschta 2007, Schmitz 2004). In many instances, the reason for the loss of top-down control is simply the local extirpation of the predator, but the strength of interspecific interactions, including top-down control, can also be mediated by resource availability, food web complexity, and productivity (Buse et al. 1999; Ritchie 2000; Moon and Stiling 2002; Finke and Denno 2004; Rothley and Dutton 2006).

Additionally, while changes to local or global environmental conditions are commonly expected to have direct effects on some or all species in a community (Asner et al. 2006; Quero et al. 2006), recent works have drawn attention to the effects of environmental change on species interactions (Whitham et al. 2006; Klanderud and Totland 2007; Spiller and Schoener 2008). For example, Tylianakis et al. (2007) found dramatic changes in food-web structure largely independent of species richness along a habitat modification gradient, and Buse et al. (1999) recorded variations in multi-species interactions as a function of

temperature. It has also been demonstrated that species interactions can mediate the consequences of climate change (Suttle et al. 2007).

I was particularly interested in how shade may affect the top-down control of predator spiders (including members of the Families Thomisidae, Lycosidae, and Salticidae) on prey grasshoppers (*Melanoplus sanguinipes*) in a field in Burnaby, British Columbia. Currently, the site's vegetative community is dominated by herbaceous, early successional grasses, and forbs (see Rothley and Dutton 2006); however, individual plants of a woody exotic species, scotch broom (*Cytisus scoparius*), have begun to appear. Scotch broom possesses several adaptations, such as rapid growth, hearty seeds, and tolerance for poor soils, which have facilitated its invasion into field and rural sites in North America (Invasive Plant Council of BC 2008). Scotch broom is also a tall, dense, shrub that casts a dark shadow. I wanted to know if the scotch broom's shadow might alter the interactions between spiders and grasshoppers, and whether these altered interactions could yield conditions that might affect the invasion of scotch broom.

In an earlier cage-based study in the same field system, grasshoppers in full sun reduced their food intake rates in response to predation risk from spiders, but did not respond to spiders when shaded (i.e., a significant shading x spider interaction; Rothley and Dutton 2006). While intriguing, this finding may have been influenced by the unnatural caged environment in which spiders and grasshoppers could not leave the cages and their densities were constant. For the study described here, I wanted to see if shading produced a similar pattern in

a more natural experiment without cages, where herbivores and predators were free to enter or leave the vegetative plots at will.

My hypothesis was that spiders in full sun would exert strong top-down control on grasshoppers (Fig. 3.1), while shading similar to that created by scotch broom would release the grasshoppers from top-down control (Fig. 3.2). My prediction was, therefore, that vegetation density in plots in full sun would be higher than vegetation density in shaded plots. In order to isolate the effects of the shade itself on the plants I compared the vegetation density in shaded plots where herbivory was excluded with the vegetation in unshaded plots where herbivory was excluded.

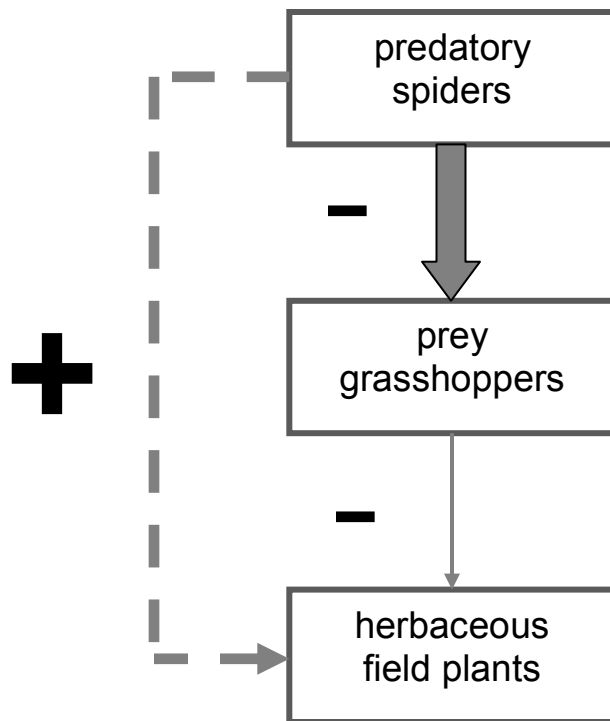


Figure 3.1 In the absence of shading, predator spiders' strong, negative top-down effect on the grasshoppers minimizes the grasshoppers' damage to the herbaceous field plants. This yields an indirect, positive effect between the spiders and the plants.

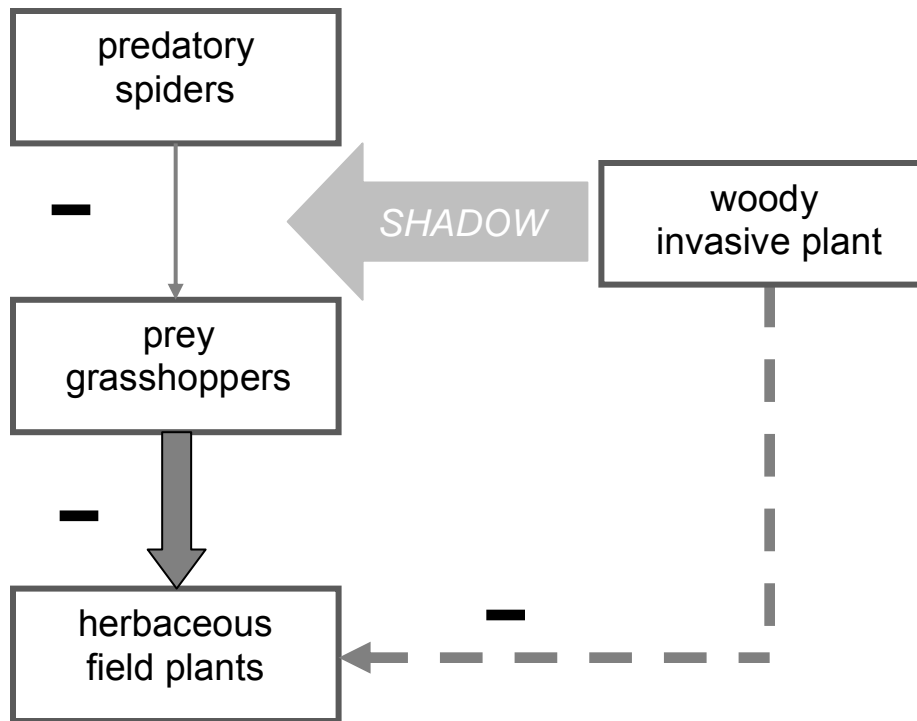


Figure 3.2 In the shadow of the invading woody plant, the predator spiders' top-down effect on the grasshoppers is reduced, and grasshoppers have a significant negative impact on the herbaceous field plants. This mediation of the interaction between the spiders and the grasshoppers results in an indirect, negative effect of the woody invasive plant on the herbaceous plants with which it competes.

3.3 Methods

The two independent variables for the experiment were herbivory and shading. I assigned thirty-two 0.25m x 0.25m plots in the field using a randomized, block design to one of four treatments: 1) no shade, no herbivory, 2) shade, no herbivory, 3) no shade, herbivory, and 4) shade, herbivory. For treatments 1 and 2, herbivory was excluded with 1m tall cages constructed of aluminum screen. Spiders were excluded from these cages, potentially confounding the treatments; however, no effect of the spiders on the vegetation was expected. I created the shading treatment by stapling black Teflon®

screening to the cage fronts for treatment 2 and I stapled the screening to two 1m tall posts along the south edge of the plots for treatment 4. I confirmed that the light, temperature, and wind conditions in the shadow of the Teflon® screens were similar to those in the shadow of the scotch broom. Sixteen additional plots were assigned to one of two sham control cage treatments: 5) no shade, cage front, and 6) shade, cage front to account for the potential contribution of the south facing panels of the cages in treatments 1 and 2 to the measured effects.

The dependent variable was the density of plant material in the plots. The plots were left for twenty days after which we clipped, dried (at 65 degrees Celsius for 24 hours), and weighed all vegetation in the plots. Although several other herbivorous insect species occur in the field, *M. sanguinipes* is the largest bodied and overwhelming numerical dominant. I therefore assumed that any effects of the herbivory treatment could be mainly associated with these grasshoppers. Similarly, while I occasionally saw other insect predators such as birds in the field, my sampling consistently revealed a vast abundance of spiders, and previous experiments had shown them to readily and voraciously consume the grasshoppers (Rothley and Dutton 2006). I therefore assumed that spiders were largely responsible for any predation related change in the grasshoppers' herbivory patterns.

Similar to Rothley and Dutton (2006), I tested for treatment effects on forb and grass plants independently. First, I logarithmically transformed the data describing the dry mass remaining in the plots at the end of the experiment to remove skewness. One record from the forb data (a treatment 4 plot) and one

record from the grass data (a treatment 1 plot) were judged to be outliers (beyond 1.5 times the width of the interquartile range outside of the interquartile range) and removed.

I used an ANOVA (α -level of 0.05) with the factors herbivory exclusion cage type (no cage, cage front only, or full cage), shading (yes or no), and shade x cage type (the interaction terms) to assess the effects of these factors on forb and grass density. Finally, I conducted pairwise t-tests to compare the four treatments of particular interest (described below). For these comparisons, I used an α -level of 0.0125 to assess the significance based on an α -level of 0.05 adjusted by a Bonferroni correction for 4 independent tests.

3.4 Results

Using an ANOVA model for final forb abundance in the plots, I found that the cage and shade treatments had an effect ($F_{5,41}=3.60$, $P<0.01$; Fig. 3.3a). For plots with no cage there was a significant decrease in the remaining amount of forbs (based on the sign and significance of the parameter estimate from ANOVA; $t=2.01$, $P=0.05$). There was also a significant interaction between shading and cage absence ($t=2.01$, $P=0.05$). When there was no shade and no cage, herbivory was relatively low, but when the non-cage plots were shaded, herbivory was very high (in fact, treatment 4 had the lowest average remaining forb abundance of any treatment). The cage front (sham control) had a significant

positive effect on final forb abundance ($t=2.15$; $P=0.04$), but the interaction between cage front and shade was not significant ($t=0.30$, $P=0.77$).

There was no detected difference between forb abundance remaining in the shaded and unshaded herbivore exclusion plots (treatments 1 and 2; $t=0.47$, $P=0.65$). No grasshopper herbivory was detected on forbs in the absence of shade (treatments 1 and 3; $t=1.26$, $P=0.23$), while in the shade grasshopper herbivory had a significant negative impact (treatments 2 and 4; $t=2.54$, $P=0.0119$). The average final forb density in the uncaged, shaded plots (treatment 4) was lower than in the uncaged, unshaded plots (treatment 3; $t=3.48$, $P=0.0018$).

The ANOVA model for remaining grass abundance was not significant ($F_{5,41}=0.84$, $P=0.53$), nor were any of the model factors (Fig. 3.3b).

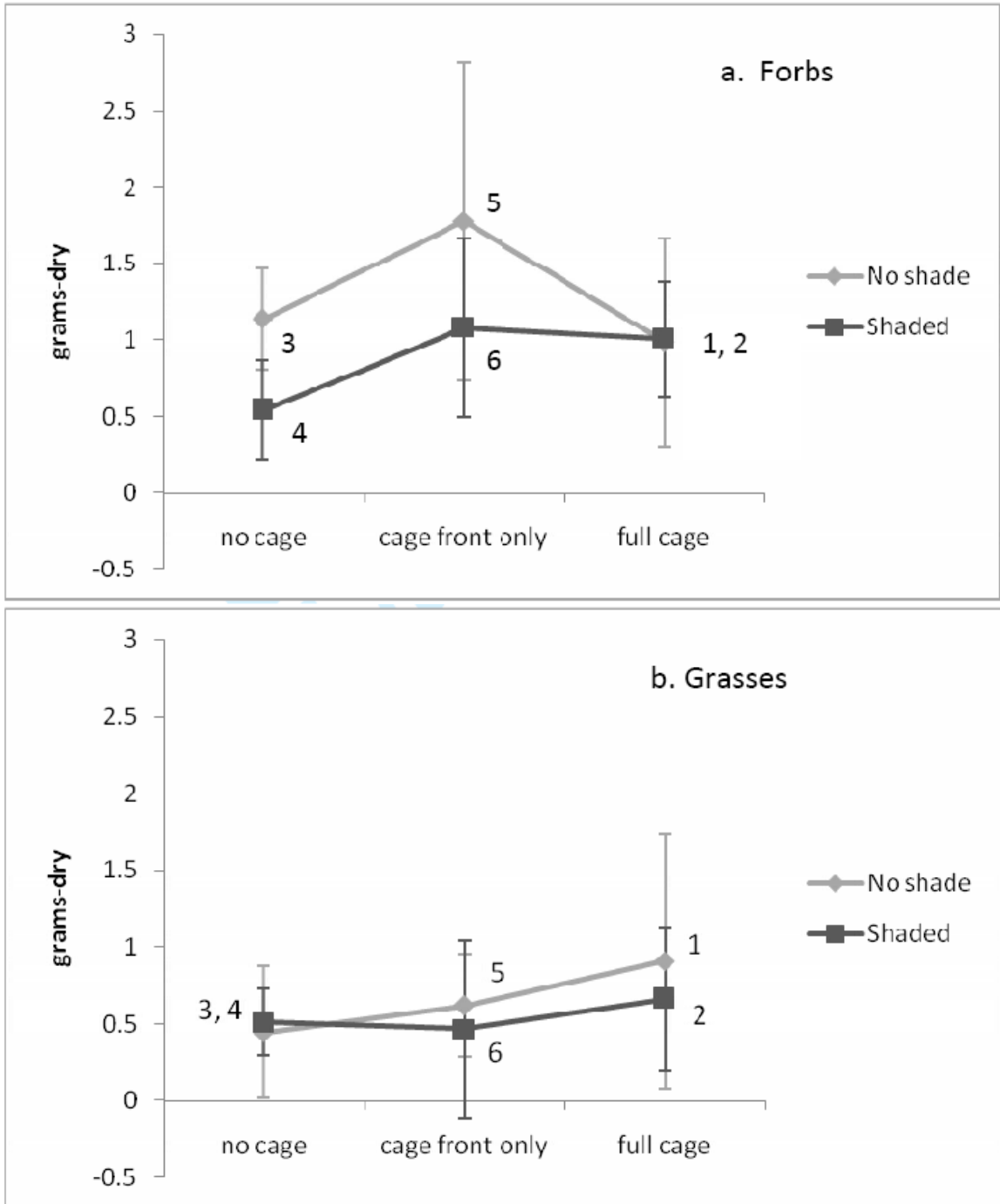


Figure 3.3 The average remaining dry weight in unshaded and shaded plots are indicated by gray diamonds and black squares, respectively, for: a) forbs and b) grasses. Error bars indicate \pm one standard deviation.

3.5 Discussion

In a previous cage-based experiment, Rothley and Dutton (2006) observed that shading reduced the top-down control of predator spiders on herbivore grasshoppers. Here, I found shading had a similar effect in more natural conditions, where both spiders and grasshoppers were free to enter and leave the experimental plots. As would be expected, the herbivore exclusion cages had a positive effect on forb density in the field plots. Conversely, shading had a negative effect on the remaining amount of forbs. The reduced forb density was not the result of a direct effect of the shade on the plants, as there was no detected difference between density remaining in the shaded and unshaded herbivore exclusion plots (treatments 1 vs. 2, Fig. 3.3a); rather, it was a consequence of higher herbivory in the shaded plots. Exactly analogous to the results of the earlier cage-based experiment, no grasshopper herbivory on forbs was detected in the absence of shade (treatments 1 vs. 3, Fig. 3.3a), while in the shade grasshopper herbivory had a significant negative impact on the plants (treatments 2 vs. 4, Fig. 3.3a).

Also similar to previous experiments, no significant effects of the treatments were detected on the grasses. I was surprised by the significant decrease in herbivory caused by the cage front (sham control) treatment (compare treatments 5 and 6 with treatments 3 and 4, Fig. 3.3a), and speculate that perhaps the grasshoppers avoided the novel objects.

The first question is, then, why was herbivory highest in the shade? For the cage-based experiments (Rothley and Dutton 2006), shading mediated the

risk response of the grasshoppers (the significant shading x spider interaction) via altered food intake rates, and it is reasonable to conclude that shading produced a similar effect in this field experiment (the significant shading x herbivory exclusion interaction). Not only was forb density lowest in the shaded, uncaged plots (treatment 4, Fig. 3.3a), but these plots also had the highest average remaining percent biomass of grass (50% compared to 25% in the unshaded, uncaged plots) of any treatment, suggesting that grasshoppers in these plots ate a high forb diet that was associated with low risk by Rothley and Dutton (2006).

However, unlike the cage-based study, grasshoppers were free to enter or leave the plots, and spiders could both scare and kill the grasshoppers. Therefore, other mechanisms that might have contributed to the shade's indirect effect on the plants must be considered. One possibility is that shading raised grasshopper intake rates, although other experiments conducted with these grasshoppers have shown that temperature is positively, not negatively, associated with intake (Rothley and Dutton 2006). A second possibility is that the grasshoppers, independent of risk, prefer the shaded plots. This is unlikely given that growth, development, and egg pod production increase with temperature (Willott and Hassall 1998). Other possible mechanisms are: 1) grasshoppers exhibited a lower risk response, in the form of higher intake rates, because spiders left the shaded plots, 2) spiders ate fewer grasshoppers in the shade, and 3) grasshoppers were attracted to the shaded plots because they perceived lower risk levels. While the need to minimize disturbance to the plots precluded

my ability to collect data regarding the role of these three mechanisms, evidence of their existence would further support my conclusion that shading mediated the top-down control of the predator.

A second question is how do I know spiders were even involved in the observed relationship between shading and herbivory when there was no predator exclusion treatment? Perhaps grasshoppers do seek shaded foraging opportunities, and then behave as if risk levels are low (high foraging rates and relatively low grass intake) even if spiders are not present. To address this, I must rely on the data from Rothley and Dutton (2006) where there was no significant difference between shaded and unshaded cages in grass ($t=0.487$, $P=0.63$) or forb ($t=0.465$, $P=0.65$) herbivory in the absence of predators (Fig. 2 in Rothley and Dutton 2006). By analogy, I conclude that the shading affected the top-down control of the predators and not the herbivores directly.

Finally, I need to consider what consequences shade-mediated, top-down control may have for the invasive scotch broom. The performance of individual plants can be influenced by neighbouring plants that compete for light, water, and nutrients (Bradford et al. 2007, Milbau et al. 2007). I found that the average final total vegetation density in the uncaged, shaded plots was 34% lower than in the uncaged, unshaded plots. Therefore, a reduction in top-down control of the spiders and the associated decrease in plant density in the shadow of scotch broom have important potential benefits for the plant's invasion success.

Increased herbivory could also have negative effects on the invader if the leaves of the scotch broom were palatable to the grasshoppers. In the field

system, I never found grasshoppers on scotch broom and never observed any leaf damage that might indicate the grasshoppers were eating this plant. This suggests that the effect of the scotch broom's shadow on the spider/grasshopper interactions has only favourable consequences for its own performance. I am planning future experiments to monitor the conditions surrounding and success of scotch broom plants over the course of a growing season.

Other examples show that organisms can alter microclimate conditions in a manner that promotes their persistence (Heil and Brunsting 1985), though my results represent the first evidence that this facilitation may occur in the form of mediated top-down control. My data also supports the growing realization that an understanding of species interactions is critical to predicting the response of ecosystems to perturbed environments (Davis et al. 1998, Fox and Morin 2001, Bai et al. 2004, Ives and Cardinale 2004, Agrawal et al. 2007, Brooker et al. 2007, Sutherst et al. 2007, Suttle et al. 2007).

CHAPTER 4: DISCUSSION

4.1 Implications for Wildlife Management

This purpose of this project was to examine how perturbations to the environment, whether from direct human influences or through indirect means, such as the introduction of invasive species, affect predator-prey interactions. In Chapter 2, I showed that grasshoppers responded to human disturbance in a way that was similar to the way that they respond to predation risk from their natural spider predators. The human disturbance treatment caused the grasshoppers to alter their foraging behaviour (a TMI), thus increasing their mortality rate and causing a trophic cascade resulting in a change in the vegetation composition (a TMII). The experiment outlined in Chapter 3 demonstrated that shading, similar to shade cast by an overtopping vegetative invasive species, can reduce the top-down control that predatory spiders have on herbivorous grasshoppers, leading to a negative indirect effect on the plant resources (a TMII).

Though these results are interesting on their own, what implications can they have for real world environmental and wildlife managers? First, both experiments help to reinforce the important roles of TMI and TMII in ecosystems. Even though TMII are often difficult to detect and quantify, a significant amount of

research has consistently shown that they can have significant ecological effects (see Preisser et al. 2005). By increasing our understanding of food web dynamics and species interactions, wildlife managers can have more developed and complete information that can be utilized to make effective management decisions.

Though small-scale study systems, such as the one used in the above experiments, may not appeal to large-scale wildlife managers directly, the information that these study systems can provide about the fundamental mechanisms of species interactions are relevant and valuable. I showed that humans can invoke anti-predator behaviour that has a number of important implications, especially when it comes to the utilization of protected areas as the means of ecosystem protection.

In the experiment in Chapter 2, I subjected the grasshoppers to infrequent (30 seconds twice a day) human disturbance treatments and found a significant result on the behaviour and mortality of grasshoppers leading to changes in the structure and composition of the vegetation. Over time, if species are continually subjected to human disturbance, there is the possibility that they would become habituated; however, they could show the opposite response and be affected even more significantly. Therefore, managers need to keep in mind that activities such as development, transportation, and recreation in, or near, protected areas may have profound effects on species interactions and overall ecosystem health. As some human activities, such as airplane traffic or sound pollution, can

penetrate protected area boundaries, protected areas may not be as effective as wildlife managers perceive them to be.

Understanding how species interactions change in response to altered abiotic conditions is important when making management decisions. If species, such as scotch broom, can facilitate their own invasion by altering the microclimate and, in turn, the trophic dynamics of the ecosystem, then more attention needs to be paid to the mitigation or eradication of invasive species. If the mechanisms behind the success of invasive species are more fully understood, ecosystem managers will have the tools to design more effective management strategies.

4.2 Future Directions

Although the above experiments answered the research questions that were posed, there are many follow-up studies that could be performed to further explore the effects of disturbance on species interactions. Though I demonstrated that human disturbance impacted the behaviour and mortality of the grasshoppers in a similar manner to how they responded to the presence of a predator, my experimental design did not allow me to actually observe and categorize the grasshopper's behaviour into specific activities (such as time spent foraging, jumping, being vigilant etc). Cameras could be used to document this behaviour in order to better understand the mechanisms behind the results observed.

Furthermore, the human induced disturbance experiment took place in small cages within a greenhouse setting. It would be interesting and invaluable to know if grasshoppers would respond to human disturbance with the same magnitude in a natural field setting. Similarly, I used unnatural shading screens to emulate the shade that an invasive woody species would produce to investigate the effects on trophic dynamics. Though the screens produced conditions that were similar in temperature, light, and wind, there may be other unforeseen abiotic conditions (such as the scent of the plant) that may alter the results observed. Therefore, with more time and resources, a similar experiment that directly incorporates the invasive plant as one of the treatments may produce more even more meaningful results.

4.3 Conclusion

As the footprint that human activity is having on the earth continues to grow, pristine, untouched habitats are becoming rare and plant and wildlife species are forced to adapt. As we attempt to find ways to mitigate or reduce the direct effects that humans are having on specific species and habitats, we need to keep in mind that ecosystems are comprised of a number of interrelated species and systems. By advancing our understanding of how species interactions are affected by human and environmental disturbance, we can make more informed management decisions that will be as effective and successful as possible.

REFERENCE LIST

- Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. *Ecology* **74**:726-733.
- Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *American Naturalist* **146**:112–134.
- Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P.J. Hudson, J. Maron, K. A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M. G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology* **5**:145-152.
- Asner, G.P., R. E. Martin, K. M. Carlson, U. Rascher, and P. M. Vitousek. 2006. Vegetation–climate interactions among native and invasive species in Hawaiian rainforest. *Ecosystems* **9**:1106-1117.
- Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* **431**:181-184.
- Barry, M. 1994. The costs of crest induction for *Daphnia carinata*. *Oecologia* **97**:278–288
- Beale, C. M., and P. Monaghan. 2004. Human disturbance: people as predation-free predators? *Journal of Applied Ecology* **41**:335-343.
- Bradford, M. A., H. B. Schumacher, S. Catovsky, T. Eggers, J. E. Newington, and G. M. Tordoff. 2007. Impacts of invasive plant species on riparian plant assemblages: interactions with elevated atmospheric carbon dioxide and nitrogen deposition. *Oecologia* **152**:791-803.
- Brooker, R. W., J. M. J. Travis, E. J. Clark, and C. Dytham. 2007. Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of theoretical biology* **245**:59-65.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**:999-1014.

- Buse, A., S. J. Dury, R. J. W. Woodburn, C. M. Perrins, and J. E. G. Good. 1999. Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology* **13**:74-82.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**:783-786.
- Davis, N. E., D. J. O'Dowd, P. T. Green, and R. Mac Nally. 2008. Effects of an Alien Ant Invasion on Abundance, Behavior, and Reproductive Success of Endemic Island Birds. *Conservation Biology* **22**:1165-1176.
- Dill, L. M., M. R. Heithaus, and C. J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* **84**:1151–1157.
- Downes, S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* **82**:2870–2881.
- Dunn, A. M., J. T. A. Dick, and M. J. Hatcher. 2008. The less amorous Gammarus: predation risk affects mating decisions in *Gammarus duebeni* (Amphipoda). *Animal Behaviour* **76**:1289-1295.
- Estes, J. A., and J.F. Palmisano. 1974. Sea Otters: their role in structuring nearshore communities. *Science* **185**:1058-1060.
- Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. *Bioscience* **55**:399-407.
- Fernández-Juricic, E., A. Sallent, R. Sanz, and I. Rodríguez-Prieto. 2003. Testing the risk-disturbance hypothesis in a fragmented landscape: nonlinear responses of house sparrows to humans. *The Condor* **105**:316-326.
- Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. *Nature* **429**:407-410.
- Foot, A. D., R. W. Osbornet, A. R. Hoelzel. 2004. Environment: Whale-call response to masking boat noise. *Nature* **428**:910-910.
- Fox, J.W., and P. J. Morin. 2001. Effects of intra- and interspecific interactions on species responses to environmental change. *Journal of Animal Ecology* **70**:80-90.
- Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**:11 [online: http://www.consecol.org/vol6/iss_1/art11].

- Gavin, S. D., and P. E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as predation risk? *Canadian Journal of Zoology* **84**:1775-1780.
- Gonzalez-Varo, J. P. J. Arroyo, and A. Aparicio. 2009. Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (*Myrtus communis*). *Biological Conservation* **142**: 1058-1065.
- He, F. L. 2009. Price of prosperity: economic development and biological conservation in China. *Journal of Applied Ecology* **46**:511-515.
- Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* **86**:2135-2144.
- Heil, G. W., and A. M. H. Brunsting. 1985. The role of nutrients in the interactions between a herbivorous beetle and some competing plant-species in the heathland. *Oikos* **44**:23-26.
- Invasive Plant Council of BC. 2008. Targeted Invasive Plant Solutions: Scotch Broom. [online] Available from http://www.invasiveplantcouncilbc.ca/publications/TIPS/Scotch_Broom_TIPS.pdf [accessed June 14, 2009].
- Ives, A. R., and B. J. Cardinale. 2004. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* **429**:174-177.
- Jarnevich, C. S., and T. J. Stohlgren. 2009. Near term climate projection for invasive species distributions. *Biological Invasions* **11**:1373-1379.
- Klanderud, K., and O. Totland. 2007. The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos* **116**:1279-1288.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* **437**:880-883.
- Křivan, V., and O. J. Schmitz. 2004. Trait and density mediated indirect interactions in simple food webs. *Oikos* **107**:239-250.

- Leung, G. P. C., B. C. H. Hau, and R. T. Corlett. 2009. Exotic plant invasion in the highly degraded upland landscape of Hong Kong, China. *Biodiversity and Conservation* **18**:191-202.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619-640.
- Lindenmayer, D. B. 2009. Forest Wildlife Management and Conservation. *Year in Ecology and Conservation Biology 2009* **1162**:284-310.
- Milbau, A., D. Reheul, B. De Cauwer, and I. Nijs. 2007. Factors determining plant-neighbour interactions on different spatial scales in young species-rich grassland communities. *Ecological Research* **22**:242-247.
- Moksnes, P. O., M. Gullstrom, K. Tryman, and S. Baden. Trophic cascades in a temperate seagrass community. *Oikos* **117**:763-777.
- Moon, D. C., P. Stiling. 2002. The effects of salinity and nutrients on a tritrophic salt-marsh system. *Ecology* **83**:2465-2476.
- Moore, M. J. C., and R. A. Seigel. 2006. No place to nest or bask: Effects of human disturbance on the nesting and basking habits of yellow-blotched map turtles (*Graptemys flavimaculata*). *Biological Conservation* **130**:386-393.
- Morrison, L. 1999. Indirect effects of phorid fly parasitoids on the mechanisms of interspecific competition among ants. *Oecologia* **121**:113-122.
- Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. *Journal of Animal Ecology* **49**:666-685.
- Parsons, D. M., and D. B. Eggleston. 2006. Human and natural predators combine to alter behavior and reduce survival of Caribbean spiny lobster. *Journal of Experimental Marine Biology and Ecology* **334**:196-205.
- Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences of the United States of America* **98**:3904-3908.
- Peters, K. A., and D. L. Otis. 2005. Using the risk-disturbance hypothesis to assess the relative effects of human disturbance and predation risk on foraging American Oystercatchers. *The Condor* **107**:716-725.

- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* **86**:501-509.
- Quero, J. L., R. Villar, T. Marañón, and R. Zamora. 2006. Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. *New Phytologist* **170**:819-834.
- Ripple, W. J., and R. L. Breschta. 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* **138**:514-519.
- Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* **95**: 361–370.
- Ritchie, L. E., M. G. Betts, G. Forbes, and K. Vernes. 2009. Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. *Forest Ecology and Management* **257**: 1920-1929.
- Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology* **81**:1601-1612.
- Rode, K. D., Farley, S. D. and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation* **133**:70-80.
- Rothley, K. D. 2002. Use of multiobjective optimization models to examine behavioral trade-offs of white-tailed deer habitat use in forest harvesting experiments. *Canadian Journal of Forest Research* **32**:1275-1284.
- Rothley, K. D., and G. Dutton. 2006. Behavioral responses to environmental change alter the direct and indirect trait-mediated interactions. *Canadian Journal of Zoology* **84**:1053-1058.
- Rothley, K. D., O. J. Schmitz, and J. L. Cohon. 1997. Foraging to balance conflicting demands: novel insights from grasshoppers under predation risk. *Behavioral Ecology* **8**:551-559.
- Schmitz, O. J. 2004. Perturbation and abrupt shift in trophic control of biodiversity and productivity. *Ecology Letters* **7**:403-409.
- Schmitz, O. J. 2005. Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management. *Oecologia* **145**:225-234.

- Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* **78**:1388-1399.
- Schmitz, O. J., and K. B. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. *Ecology* **82**:2072-2081.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**:153-163.
- Semeniuk, A. D., B. Speers-Roesch, and K. D. Rothley. 2007. Using fatty-acid profile analysis as an ecological indicator in the management of tourist impacts on marine wildlife: a case of stingray-feeding in the Caribbean. *Environmental Management* **40**:665-677.
- Sergio, F., I. Newton, and L. Marchesi. 2005. Conservation: Top predators and biodiversity. *Nature* **436**:192-192.
- Songer, M., M. Aung, B. Senior, R. DeFries, and P. Leimgruber. 2009. Spatial and temporal deforestation dynamics in protected and unprotected dry forests: a case study from Myanmar (Burma). *Biodiversity and Conservation* **18**: 1001-1018.
- Spiller, D. A., and T. W. Schoener. 2008. Climatic control of trophic interaction strength: the effect of lizards on spiders. *Oecologia* **154**:763-771.
- Stirling, I., and C. L. Parkinson. 2006. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* **59**:261-275.
- Sutherst, R. W., G. F. Maywald, and A. S. Bourne. 2007. Including species interactions in risk assessments for global change. *Global Change Biology* **13**:1843-1859.
- Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. *Science* **315**:640-642.
- Tarlow, E. M., and D. T. Blumstein. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science* **102**:429-451.
- Torres-Porras, J., J. Carranza, and J. Perez-Gonzalez. 2009. Selective culling of Iberian red deer stages (*Cervus elaphus hispanicus*) by selective monteria in Spain. *European Journal of Wildlife Research* **55**:117-123.

- Trussell, G. C., P. J. Ewanchuk, and C. M. Matassa. 2006. Habitat effects on the relative importance of trait and density-mediated indirect interactions. *Ecology Letters* **9**:1245-1252.
- Tuxbury, S. M., and M. Salmon. 2005. Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biological Conservation* **121**:311-316.
- Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* **445**:202-205.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494-499.
- Webb, N. W., and D. T. Blumstein. 2005. Variation in human disturbance differentially affects predation risk assessment in western gulls. *The Condor* **107**:178-181.
- Werner, E. E and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**:1083-1100.
- Whitham, T. G., J. K. Bailey, J. A. Schweitzer, S. M. Shuster, R. K. Bangert, C. J. LeRoy, E. V. Lonsdorf, G. J. Allan, S. P. DiFazio, B. M. Potts, D. G. Fischer, C. A. Gehring, R. L. Lindroth, J. C. Marks, S. C. Hart, G. M. Wimp, and S. C. Wooley. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics* **7**:510-523.
- Willott, S. J., and M. Hassall. 1998. Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. *Functional Ecology* **12**:232-241.
- Xu, J. C., R. E. Grumbine, A. Shrestha, M. Eriksson, X. F. Yang, Y. Wang, and A. Wilkes. The Melting Himalayas: Cascading Effects of Climate Change on Water, Biodiversity, and Livelihoods. *Conservation Biology* **23**:520-530.
- Yasue, M., and P. Dearden. 2006. The potential impact of tourism development on habitat availability and productivity of Malaysian plovers *Charadrius peronii*. *Journal of Applied Ecology* **43**:978-989.