## THE IMPORTANCE OF ABIOTIC CHANGES ON PLANT AND ANIMAL COMMUNITY INTERACTIONS

by

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### ABSTRACT

Experiments were conducted in both greenhouse and field settings using a three trophic level system to determine whether abiotic changes alone could alter predator-prey-resource interactions, the relative contribution of traitmediated and density-mediated effects, and trait-mediated and density-mediated impact intensity under varying abiotic conditions. Three manuscripts were produced; the first describes how grasshoppers altered their diet under changed light and temperature conditions in a field setting; the second explains an experiment that demonstrated that non-lethal predators can have as large an effect as those that are lethal; the third shows how light and shade can change the magnitude of trait- and density-mediated interactions and their relative contributions. Resource managers must think about the potential threats to protected areas such as global warming and development and the impact of abiotic changes on plant and animal communities in order to predict their consequences.

**Keywords:** Abiotic factors; Climate change; Consumptive effects; Densitymediated indirect interaction; Food web; Global warming; Non-consumptive effects; Trait-mediated indirect interaction; Trophic cascade; Trophic level; Wildlife management

**Subject Terms:** Ecosystem management; Nature conservation; Wildlife; Food chains

### **EXECUTIVE SUMMARY**

Anthropogenic disturbances negatively impact animals due to *physical* changes in habitat structure and the resources on which they depend. To determine if species' interactions can also be affected by *abiotic* factors associated with disturbance, experiments were conducted in both greenhouse and field settings on a three trophic level system using a top predator (spider), intermediary prey species (grasshopper), and resource (grasses and forbs). Light and temperature were selected as abiotic factors for manipulation.

Three manuscripts were produced as a result of the experiments; the first describes how grasshoppers altered their diet under changed light and temperature conditions in a field setting; the second demonstrates that non-lethal predators can have as large an effect as those that are lethal; the third shows the influence of changed light and temperature on the magnitude of trait and density-mediated interactions and their relative contributions to reduced foraging.

Managers of wildlife must think about how climate change and associated fluctuations in light, temperature and other non-physical alterations in the environment will impact target species if they wish to maintain ecosystem health and population persistence. Additionally, the potential effects of abiotic changes on plant and animal communities must be considered when planning and development take place near parks and protected areas, and managers have to know that trophic cascades can be caused by physical and non-physical factors.

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For Julie.

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# GLOSSARY

Abiotic factors	Nonliving components of the biosphere such as weather, chemical and geological factors, light, temperature
Climate change	Refers to the climatic changes currently ongoing on global scale
Consumptive effect	Density-mediated interaction, wherein one organism kills or consumes another
DMII	Density-mediated indirect interaction between two trophic levels at least one step removed from each other, resulting from a consumptive effect
Food web	The suite of organisms between which energy flows via consumption
Global warming	Increases in the average temperature of the earth's air and oceans in recent decades and its projected continuation
Non- consumptive effect	Trait-mediated interaction, wherein the behaviour of one organism causes another to alter its behaviour
ТМІІ	Trait-mediated indirect interaction between two trophic levels at least one step removed from each other, resulting from a non-consumptive effect
Trophic cascade	The U-shaped pattern that results when an intermediary species reduces consumption of a lower trophic level, releasing the next lower trophic level from predation
Trophic level	The level or guild of organisms from which energy is transferred to another via consumption
Wildlife Management	The process of maintaining wildlife populations at desired levels, as determined by wildlife managers

### **CHAPTER 1: INTRODUCTION**

### 1.1 Context and Organization of this Document

This document is a publication-based project. Chapter 1 is a general introduction that describes the rationale and novelty of this work and its objectives, along with background on trait and density effects and disturbance. Two manuscripts (Rothley and Dutton 2006 and Rothley and Dutton 2007 – in review) will be referred to throughout this document, as their findings are relevant to the subject at hand. Because they are part of the outcome of the work conducted on this project and are relevant to the subject at hand, they are reproduced below (Section 1.8 and 1.9), in brief.

Chapter 2 describes an experiment conducted as part of this project in a manuscript form, and is one of three such manuscripts that were the outcome of this project. This chapter contains an introduction, methods, results, and discussion; the discussion section in this chapter pertains solely to that particular manuscript.

Chapter 3 is a general discussion chapter. Implications of the results from all three manuscripts are described here, as they relate to wildlife management in parks and protected areas, specifically the threats of global warming and planning and development. Tables are presented to help managers in understanding food web structure and recognizing potential impacts of abiotic

changes and how they might affect species interactions. Additionally, drawbacks to this study and future directions are considered.

#### 1.2 Rationale and Novelty of this Work

As human populations continue to grow and human development expands into previously undisturbed areas, plant and animal communities come under siege. For a manager of a wildlife area, understanding how different species in the same community respond to disturbances is key to knowing what management practices to prescribe for different scenarios. This means having an intimate knowledge of the biology of target species and their behaviours, and identifying potential threats. Up to this point in time, focus has been on how human disturbances directly alter habitat or reduce numbers of animals, through the destruction of habitat or harming of animals and their resources (Cushman 2006, Fischer and Lindenmayer 2007). Recently, the importance of traitmediated interactions (non-consumptive effects) and trait-mediated indirect interactions (TMIIs) has been recognized regarding their influence on community dynamics (Werner and Peacor 2003, Jonsson et al. 2007), and it is essential for managers to understand these interactions in the context of disturbance if they are to prescribe the proper management practices and possible measures for remediation.

Species in the same community can be said to belong to the same "food web," which is the suite of organisms, generally in the same geographic area, between which energy flows via consumption. Species exist on different "trophic levels," where controphic species are often in the same guild, exploit the same

resources and have the same predators (Blaustein and Chase 2007). Organisms are often described as "top" (predator), "intermediary" (prey), and "bottom" (resource) to denote their trophic position. Generally, organisms in plant and animal communities interact in two broad ways: consumptive and nonconsumptive effects. In the former, a predator organism kills or consumes prey, such that the actual density of the prey population is changed. In the latter, the prey is not consumed (there is no transfer of energy), but by changing its behaviour due to predation risk an organism may spend less time on other activities (such as foraging). Prey may adopt predator averse tactics, the costs of which can lead to reduced growth, maturation rates, survivorship, fecundity, or population growth (Abrams 1984, Werner and Peacor 2003).

Consumptive and non-consumptive effects also have associated *indirect* interactions (DMIIs and TMIIs, respectively). When an intermediary species either is killed or exhibits predator avoidance behaviour, it can reduce the foraging pressure on the prey's resource, causing the latter to increase in abundance (Figure 1). Trait and density-mediated interactions occur between two organisms, usually of different trophic levels. Trait and density-mediated *indirect* interactions involve between three or more organisms; experimental studies generally explore systems where each species is on a different trophic level, but in the real world different species on the same trophic level often interact in the same food web. A great deal of recent work has shown that TMIIs are often as important as or more important than DMIIs in shaping ecological communities (Werner and Peacor 2003, Wojdak and Luttbeg 2005, Prasad and Snyder 2006).

The strength of these interactions depends very much on the context in which they are examined; however, up to this point, that context has largely been a function of organism densities, resource levels, and habitat structure (Luttbeg et al. 2003, Bolnick and Preisser 2005, Trussell et al. 2006), as physical changes are the most obvious way that context can be changed to alter species' interactions.



Figure 1. Density-mediated interactions occur when a prey species is killed or consumed (left); trait-mediated interactions occur when prey species evade predation (right). A three-trophic-level system is pictured. Both kinds of interactions can have indirect effects (dotted arrow). Solid arrows represent the flow of energy between trophic levels. The novelty of this work is to examine how abiotic factors (nonliving components of the biosphere such as weather, chemical and geological factors, light, temperature, etc.) can alter the ways that animals interact; specifically, how the two parts of that interaction (TMIIs and DMIIs) change in occurrence and strength due to species-specific behaviours induced by said abiotic changes (Figure 2)(Table 1).



Figure 2. Abiotic factors such as light, temperature, chemicals, and pollution can alter the context in which organisms interact and influence community dynamics by changing the magnitude of consumptive and non-consumptive effects and TMIIs and DMIIs.

If the behaviour of one species in a food web is perturbed, such that they perform "behaviour A" as opposed to "behaviour B", or temporally shifted as a result of abiotic changes, the impact can reverberate through the "links" or trophic levels in a food chain and change community structure via trophic cascades (occurs when predators in food web constrain their prey's abundance or foraging behaviour, thereby releasing the resource from predation) (Chase 1996). Trophic cascades are typically a signature of top-down control, where top predator densities influence community structure, and can be caused by consumptive and non-consumptive effects (Byrnes et al. 2006, Trussell et al. 2006).

The reason consumptive and non-consumptive effects and their associated indirect effects change in magnitude under different conditions is that species in the same food web may react *differently* to the same changes (Figure 3 below); this sounds intuitive, but is of enormous consequence if species react in opposite or different ways to the same abiotic change. For instance, imagine a predator that relies on smell to detect its prey, while the prey relies on visual acuity. If increased pollution impedes sensing prey via olfaction, the predator will be at a disadvantage, while the prey can remain unaffected. Similarly, the "windows" or periods of time within which predators and prey feed during a given day may shift temporally in opposite directions or may converge, causing the occurrence of consumptive and non-consumptive effects, TMIIs and DMIIs to change (Chase 1996, Joern et al. 2006). Examining the role of abiotic factors in community interactions is particularly apt given the threat of global warming

Table 1.	How abiotic changes affect plant and animal communities.	
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Step	Event
1	Abiotic change is introduced, typically associated with some kind of disturbance
2	Organisms alter their behaviour due to physiological changes or perceived differences in their surroundings
3	Interactions (made up of consumptive and non-consumptive effects, TMIIs and DMIIs) <i>between</i> species in the same food web are altered as the relative importance of consumptive and non-consumptive effects, TMIIs and DMIIs changes
4	Community structure (in the form of changed resource levels, for example) results

(which can be thought of as large-scale disturbance) and its effect on temperature and feedback loop with albedo (Easterling 1997, King 2005, Winton 2006). Many animals use abiotic cues from their environment to tell them when to perform certain behaviours, and there is mounting evidence that climate change alters the cues that some animals use for the timing of migration (Mills 2005, Sparks et al. 2007), breeding (Millar and Herdman 2004), and hibernation (both timing and duration) (Jorgensen 1986, Reading 2007). Additionally, localized human development can bring about changes that, while not on the scale of global warming, can potentially affect organisms via abiotic factors. Structural changes to habitat (such as deforestation) can lead to fluctuations in light and temperature across the perturbed area, even when trees are retained (Heithecker and Halpern 2006). Encroaching developments at park and protected area boundaries can pose threats to wildlife not only because new edge creates abiotic microclimatic gradients for wind, temperature, and light may extend anywhere from 50 to 250 meters into forest (Chen et al. 1995). Development buffer zones may need to be adjusted to mitigate possible abiotic disturbances in the future.

Managers in parks and protected areas who are responsible for wildlife need to be cognizant of disturbances accompanied by abiotic changes and how those abiotic conditions can differentially affect species; this requires an intimate understanding of the biology of target species so that potential impacts can be predicted and measures for mitigation can be taken.

#### **1.3 Trait and Density-Mediated Interactions**

As mentioned above, organisms in the same food web interact with each other in two ways, via consumptive and non-consumptive effects (and associated TMIIs and DMIIs). Density-mediated interactions entail the death and (usually) consumption of a prey species such that its population density is changed. Trait-mediated interactions involve a modification of the prey's behaviour, such as habitat or resource selection (Huang and Sih 1991, Peacor and Werner 1997, Downes 2001), or life history (Abrams 1995, Pangle and Peacor 2006), due to predation risk. Grasshoppers, for instance, adaptively adjust their foraging behaviour to tradeoff between energy intake and time spent being vigilant in response to predation risk (Rothley et al. 1997). Both consumptive and nonconsumptive effects can have indirect interactions (DMIIs and TMIIs, respectively) between the predator and the prey's resources (in a tritrophic system). The influence of DMIIs and TMIIs has been observed in natural systems and experimentally produced in both terrestrial and aquatic communities (Chase

1996, Beckerman et al. 1997, Peacor and Werner 2001, Werner and Peacor 2003, Gimenez 2004, Ripple and Beschta 2004, Schlacher and Cronin 2006, Stief and Holker 2006). Only of late have studies concluded that TMIIs are frequently either equal to or greater in strength than DMIIs (Huang and Sih 1991, Wissinger and McGrady 1993, Schmitz 1998, Diehl et al. 2000, Werner and Peacor 2001, Werner and Peacor 2003, Luttberg and Kerby 2005, Preisser et al. 2005, Wojdak and Luttbeg 2005). The quantification of TMIIs and DMIIs has only been attempted in recent experimental studies (Huang and Sih 1991, Peacor and Werner 2001, Luttbeg et al. 2003, Damiani 2005, Trussell et al. 2006) using food webs of three trophic levels; even estimating the impact of TMIIs in more complex foodwebs is very difficult (Bolker et al. 2003) due to the co-occurrence of TMIIs and DMIIs (Relaya and Yurewicz 2002) and attenuation that can occur as more trophic levels are added to the community (Okuyama and Bolker, 2007).

Trait and density-mediated interactions and associated indirect interactions are generally thought of as alternative phenomena, but in reality often occur in tandem. For example, a predator may only consume a few or even one prey item, but its presence and activity are likely to induce risk response behaviour in the remaining prey. Additionally, trait effects could exacerbate density effects if the anti-predation behaviour exhibited by the prey results in mortality due to poor health. Experiments have successfully examined TMIIs in isolation; Schmitz (1998) restrained spider fangs so that the only kind of interaction with grasshoppers was trait-mediated, and barriers can be used so that prey organisms are aware of the predation risk but cannot be attacked

(Bernot and Turner 2001, Wojdak and Luttbeg 2005). Isolating the effects of DMIIs is much more difficult since any consumptive effect involves a nonconsumptive effect(s) as well, owing to predator avoidance response of prey prior to their capture. How to accurately estimate TMIIs, DMIIs, and TIIs (total indirect interactions) is discussed in the Materials and Methods section of Chapter 2.

Investigations have also noted that the relative importance of trait and density effects can vary, even for the same predator-prey-resource community, depending on context (Luttbeg et al. 2003, Bolnick and Preisser 2005, Wojdak and Luttbeg 2005, Trussell et al. 2006,). The TII of one trophic level on another is made up of density and trait interactions (both direct and indirect); it is possible that the sign and strength of the total effect can change if contextual alteration affects the behaviour of the study organisms. Contextual changes can be physical, such as alteration of habitat, population density, or resource level; Trussell et al. (2006) found that both the sign and the strength of DMIIs and TMIIs varied depending on whether they were measured in risky or refuge habitats, and Wojdak and Luttbeg (2005) discovered that altering resource levels affected TMII and DMII strength. Contextual changes can also be abiotic, such as fluctuations in light, temperature, climate, and pollution. Chase (1996) found that altering shade in a spider-grasshopper-resource system altered DMIIs, and Rothley and Dutton (2006) found that TMIIs in a similar spider-grasshopperresource system changed as light and temperature levels were varied.

In general, a changed context means a different risk of predation for prey species. Prey can adopt various behavioural strategies to deal with low and high

risk scenarios. In natural environments, prey organisms are likely to experience a substantial level of temporal variability in predation risk (Sih et al. 2000, Ferrari and Chivers 2006, Fraser et al. 2006). Under predation risk, prey can stay where they are using the same behavioural allocation (time spent performing certain behaviours), stay where they are but change their behaviours, move and make no change in their behavioural allocation; or move and shift their behavioural allocation (Schmitz et al. 1997). Each option is also expected to vary with respect to its fitness consequences although all will carry costs, such as a reduction in foraging time or access to favourable habitat (Lima and Dill 1990, Lima 1998, Winnie and Creel 2007). Different sites may offer varying degrees of refuge from potential predators, and foods can be highly dissimilar in their nutritional quality, required handling times, and edibility (Schmitz 1994).

How to use knowledge of TMIIs in managing wildlife is not well defined; there have only been a few specific cases where knowledge of TMIIs has been used to identify and prescribe management practices. One example is the reintroduction of the wolf in Yellowstone National Park. After being absent for nearly 70 years they were reintroduced in 1995, and within 10 years the elk population was reduced, allowing recruitment of woody browse species and beavers, due to a combination of TMIIs and DMIIs (Ripple and Beschta 2004, Ripple and Beschta 2006).

#### 1.4 Disturbance Leads to Abiotic Changes

As the human population continues to grow habitats for animals are reduced, fragmented, or eliminated. While clearly not in the best interest of

biodiversity and the animals we seek to protect in parks and protected areas, how does it relate to abiotic factors?

Small-scale disturbance includes creation of edge, when areas are cleared for construction of buildings and roads, or when formerly contiguous habitat is altered in some way, such as a land-use change from forest to agriculture. Edge has been identified as an important factor in shaping plant and animal communities (Pickett and White 1985) and its differential effects on species is well known. Edge can effectively reduce useable habitat for many native species because it creates an "unusable buffer" in which predation may be abnormally high (Turner 1996, Batary and Baldi 2004); conversely edge may be favourable for other species, depending on life-history characteristics (Schlaepfer and Gavin 2001). The creation of that edge is a *structural* change to the environment. However, there are associated changes in abiotic factors that go hand in hand with edges, such as fluctuations in light and temperature. Animals may respond directly to the edge itself, or to abiotic changes associated with the edge (Kristan et al. 2003). Increases in light, temperature, and wind are all potential "mini" disturbances associated with edge (Esseen and Renhorn 1998, Davies-Colley et al. 2000), and how animals react or behave in response to these disturbances may be species-specific (Taper et al. 1995) (Figure 3).

Large-scale disturbance also includes edge effects, but on a landscape scale such as a large clear cut (and associated abiotic changes), or, where only abiotic changes are concerned, climate change. Whether climate change should rightly be called a disturbance is open for debate, but most of the literature

agrees that it is both anthropogenically driven and disruptive (Travis 2003, von Storch and Stehr 2006), so here it will be treated as such. Abiotic changes associated with climate change include fluctuating light levels associated with albedo (Wang et al. 2006, Winton 2006), chemical and toxin redistribution (Macdonald et al. 2003, Macdonald et al. 2005), and of course, elevated temperatures (IPCC 2001).

Even where structural changes appear to be slight, as in the creation of a single trail through a previously unbroken woodland, or decreased heterogeneity of a forest due to replanting, the consequences can be severe (Bartos and Booth 1994). Here it is important to note that *structural* or *population density* changes in an environment can radically alter species' interactions for exactly the same reason *abiotic* changes can; namely, different organisms in the same food web will be differentially affected by the same disturbances. If environmental conditions are altered through disturbance it is possible that the cues prey use to determine predation risk could be changed (Orrock et al. 2004, Orrock and Danielson 2004); in turn, effects of changing interactions between predator and prey can then filter down to lower trophic levels (Bernot and Turner 2000, Dill et al. 2003).

Managers should be well aware of obvious disturbances that are structural and physical; what this study aims to do is raise awareness of the potential impacts of abiotic, non-physical factors. Since abiotic changes can accompany both structural and non-structural disturbances managers must be mindful of less obvious impacts, such as those caused by human development *outside* of

protected area boundaries. Additionally, managers typically identify and prescribe management actions based on changes *within the food web* (Karieva 1994), but the abiotic changes that accompany structural changes (if in fact there are any within the management area) may be more important than the structural change itself.



Figure 3. Disturbance can lead to abiotic changes, which in turn differentially impact species in the same food web. Solid arrows represent the flow of energy between trophic levels, and dashed line represents an indirect interaction.

### **1.5 Abiotic Factors Influence Behaviour**

Animal behaviour is generally thought of in terms of tradeoffs. Any time an organism spends doing activity "A" is time that it cannot spend to perform activity "B", thus, it must decide how to divide its time between different behaviours. The idea that behaviour plays an important part in shaping ecological communities through interspecific interactions has also gained credence recently (Mouritsen and Poulin 2005, Wojdak and Luttbeg 2005). In our study system, we assumed that there was a trade-off between foraging and vigilance behaviour in the intermediary species, the grasshopper *M. sanguinipes*, and changes to vegetation biomass were mediated by the time spent performing either action; more time spent eating meant less time being vigilant. While this trade-off has been criticized as an oversimplification (Ward 1992) we felt that foraging and vigilance were the two main avenues open to the grasshoppers in our three trophic level system where a predator and resource were present. For the predatory crab spider *Philodromidae Tibellus* we assumed the trade-off was between searching (in this case literally sitting and waiting) and striking or attacking. Although we did not measure the amount of time spent by the animals exhibiting each kind of behaviour, this evolutionary ecological principle of allocating time to different behaviours based on available information underpins much of the discussion, as we made the assumption throughout our experiments that time spent by the animals exhibiting different behaviours would lead to changed occurrences of consumptive and non-consumptive effects and TMIIs and DMIIs.

The first way that abiotic factors influence how organisms behave is through perception. In natural environments, prey organisms are likely to experience a substantial level of temporal variability in predation risk (Sih et al. 2000, Ferrari and Chivers 2006, Fraser et al. 2006), and as a result will move to new environments to reduce that perceived risk. If an abiotic change occurs (such as the introduction of higher light levels) an increased awareness of predation may cause the prey species to alter its behaviour. Changes in light intensity have been shown to alter predator perceptual abilities (Torgersen 2001, Dieguez and Gilbert 2003, Richmond et al. 2004), and if an abiotic change allows a predator in a food web to better perceive prey, the frequency of consumptive events may increase. Or, increased perception of predation risk by prey may cause non-consumptive effects and TMIIs to increase as the prey allocate more time to vigilance. This perceived environment can be thought of as the "external" information an organism uses to make decisions regarding its behaviour. The potential outcome is an altered community structure as the behavioural changes reverberate through the food chain in the form of a trophic cascade (Schmitz 2003, Trussell et al. 2004, Trussell et al. 2006).

A second way that abiotic factors influence behaviour is via physiology. Again, the internal state of the animal gives it information it uses to make a decision about how to respond to its environment. Almost all organisms have temperature thresholds above and below which bodily functions are affected. Growth rates and development, metabolism and bodily functions are all subject to temperature changes (Howell et al. 1970, Ikeda 1985, Ikeda et al. 2001, Ji et

al. 2005, Yang et al. 2005, Swanson and Thomas 2006, Luckenbach et al. 2007). Photoperiod also plays a role in timing life history stages such as diapause (Tatsumi and Takeda 2005). An organism uses this "internal" information (in conjunction with its external information) to decide whether to move to a new environment or change its behaviour.

### 1.6 Study System

The study system used for all experiments conducted for this project contained three trophic levels, with a spider as the top predator, grasshopper as the intermediary prey species, and forbs and grass vegetation the resource (Figure 4). The spider *Philodromidae Tibellus* (family, genus) is a "sit and wait" predator that generally occupies the upper part of vegetation when hunting for prey, in this case the species *Melanoplus sanguinipes*. The resource or vegetation was used as the measured indicator in all experiments for calculating TMIIs and DMIIs; a mix of grasses (mainly *Calamagrostis canadensis* (bluejoint) and *Poa pratensis* (pasture grass)) and forbs (mainly *Taraxacum officinale* (dandelion) and *Trifolium repens* (white clover)). Experiments were conducted either in a field setting or lab setting (greenhouse). The field setting is described below in Section 1.8; the lab setting is described in Section 1.9 and Chapter 2.

This study system was chosen because the relationships between the trophic levels have been well documented (Pfadt 1949, Belovsky 1986, Chase 1996, Rothley et al. 1997) and it allowed for full control of aspects of the experiments that would not have been possible in a larger system where organisms could not be manipulated; the study animals are small enough such

that cages can be used to exclude unwanted plants and animals and treated to manipulate abiotic conditions. The use of this study system was not meant to place importance on the subject species *per se*, but to use them as a model system such that the results of the experiments might be applied to other food webs with organisms of different plant and animal taxa.

The use of this study system dictated to a large degree what abiotic factors could be selected for manipulation. In this case cold blooded organisms that rely on vision were used so manipulation of light and temperature were deemed appropriate (for further discussion of the importance of knowing the behaviour of your organisms, see Section 3.1.2). Although the exact way that light influences grasshopper vision is unknown, both wavelength and intensity are known to affect how its environment is perceived (Wallace 1959, Bennett et al. 1966, Bernays and Wrubel 1985, Bailey and Harris 1991). M. sanguinipes does use olfactory cues to detect green leaf volatiles and find resources (Hopkins and Young 1990), but we felt alteration of light and temperature was concomitant with disturbance such as edge creation (small scale) or climate change (large scale). Additionally, Chase (1996) showed that a similar study system (consisting of wolf spider, grasshoppers, and plants) was affected by light and temperature in the form of grasshopper food intake. We wanted to alter abiotic factors that would affect both the predator and prey organisms. Crab spiders have been studied less intensively than grasshoppers, but we assumed that like related spiders, *Tibellus* would rely on vision to catch its prey (Heiling et al. 2005, Thery 2007).



Figure 4. The study system is made up of three trophic levels: predator, prey, and resource. The sold arrows represent the flow of energy, the dotted arrow represents an indirect effect.

#### 1.7 Research Goals and Questions

Two experiments were conducted to address three primary questions for this project.

Experiment 1 was a field-based experiment that sought to answer the question: 1) Are abiotic changes alone enough to alter the way that animals in the same food web interact with each other? An affirmative answer to this question allowed experiment 2 (below) to expand on our findings.

Experiment 2 was a greenhouse-based experiment in which several questions were addressed: 1) Can non-lethal predators can have as large an effect as those that are lethal?; 2) What is the relative intensity of TMIIs and DMIIs in the three trophic-level system and how do changes in diet in a lab experiment compare to changes in a field experiment?; and 3) How does the relative contribution of TMIIs and DMIIs change under different environmental conditions? Experiment 2 addressed a growing notion in the scientific literature that TMIIs are just as important as DMIIs, but took the additional step of actually quantifying both. The second part of Experiment 2 (Question 3) brought together parts of Question 1 and 2 by addressing how TMIIs and DMIIs change quantitatively under different abiotic conditions.

Questions 1 and 2 are addressed in section 1.8 and 1.9 below, respectively, and detailed in Rothley and Dutton 2006 (Question 1) and Rothley and Dutton 2007 (in review) (Question 2). Question 3 is detailed in Chapter 2 in the form of a full manuscript.

### 1.8 Rothley and Dutton 2006

A field study was conducted in the summer of 2005 in an old-field located on Terasen Gas property on Burnaby Mountain, Burnaby, British Columbia. The site was deemed to be appropriate because of the presence of the grasshopper *M. sanguinipes* (lesser migratory grasshopper) and spider *Philodromidae Tibellus* (crab spider) (identified to genus) as well as a mix of grasses (mainly Calamagrostis canadensis (bluejoint) and Poa pratensis (pasture grass)) and forbs (mainly Taraxacum officinale (dandelion) and Trifolium repens (white clover)). Based on observations prior to conducting the experiment M. sanguinipes appeared to be the primary consumer of vegetation; collection and identification of insect species from the site the following summer confirmed that there were no other insect species eating grasses and forbs at the same level as *M. sanguinipes.* This allowed us to assume that grazed vegetation observed post experiment could be attributed to foraging of *M. sanguinipes. Tibellus* was observed attacking and subduing *M. sanguinipes* when brought in close proximity. As avian predation on *M. sanguinipes* appeared infrequent and not to be a significant contributor to grasshopper mortality (personal observation), it was assumed most predation to *M. sanguinipes* was caused by *Tibellus*.

The question we wanted to address was: "Are trait-mediated behavioural responses to abiotic changes, alone, enough to change food web dynamics?"

Cages approximately 1 m<sup>2</sup> and 1m tall were set up at the field site to determine whether increases in light and temperature were capable of altering food web dynamics (Figure 5). High light and high temperature treatments

represented a "disturbed" environment, where their increase could be due to the creation of edge; low light and low temperature represented a pre-disturbance environment. A random block design was used to assign cages to the following treatments:

H: no animals, high light/temperature, 2) L: no animals, low light/temperature,
GH: grasshoppers only, high light/temperature, 4) GL: grasshoppers only, low
light/temperature, 5) GSH: grasshoppers and spiders, high light/temperature, and
GSL: grasshoppers and spiders, low light/temperature.

The grasshoppers used were 4<sup>th</sup> instar to ensure that they could not actually be eaten by the spiders owing to their large size. This was confirmed by placing grasshoppers of different instars into a jar with *Tibellus*; grasshoppers at 2<sup>nd</sup> instar and below were successfully subdued, 4<sup>th</sup> and 5<sup>th</sup> instar grasshoppers were either not attacked or were unharmed by attempted assaults. Each cage contained a mix of forbs and grasses. After one week the cages were removed, the animals released, and the vegetation clipped, dried, and weighed.



Figure 5. Field site and experimental setup for experiment 1 (photo by the author).

Differences in resource biomass were determined between the treatments.

A least squares fit ANOVA model shows that the main effects of "shading" (P=0.37) and "spider" (P=0.73) were not significant on daily forb consumption, but that the interaction "shading\*spider" (P=0.01) was significant. There was no significant relationship between the effects and daily grass consumption. Comparing the data by treatment, GSH grasshoppers ate less forbs than GSL (P=0.02) and GH (P=0.05) grasshoppers (Figure 6). There were no differences in mean grass consumed between treatments.



Figure 6. Grasshoppers' daily per capita grass and forb intake in unshaded (GH), in shaded (GL), in shaded with spiders (GSL), and in unshaded with spiders (GSH). Bars show standard errors. Note that in some instances the values are negative because these are relative intake rates calculated with respect to the one-trophic level control cages.

In unshaded conditions in response to spiders, grasshoppers reduced their energy intake by 90%, reduced their time spent feeding by 68%, and switched to a largely grass diet that should increase mortality, while in shaded conditions spiders induced no diet shift. The results indicated that without changing the resource level or abundances or densities of the animals in any
way (that is, without altering the food web components at all), food web dynamics, as indicated by resource biomass, can change markedly under changed abiotic conditions (Figure 7). The result observed of a trophic cascade pattern under conditions with higher light and temperature is entirely consistent with other findings such as those of Khan et al. (2003), Moran and Hurd (1998), and Ripple and Beschta (2004), with the difference that our manipulations were non-structural with no changes made to the trophic components of the study system. The significant decrease of forb consumption in unshaded cages versus shaded cages suggests that grasshoppers may be less aware of predator presence in shaded cages. Although the increase of forb consumption in shaded cages in the presence of a predator is unusual, it was not significant.



Figure 7. Forb (left) and grass (right) abundance remaining in the cages at the end of the experiment in one-, two-, and three-level trophic systems in the unshaded (top) and shaded (bottom) conditions. Forb consumption under shaded and unshaded treatments (left) shows a different resource biomass pattern versus no change in consumption pattern for grass (right).

Consistent with Chase (1996), our findings highlight the importance of abiotic factors associated with disturbance and suggest that they may alter food web dynamics in the same way that structural changes can. Although Chase found an decrease in consumption under shaded conditions, we found a decrease under unshaded conditions. Further studies are needed to determine whether behavioural changes exhibited by either predator or prey are due to light or temperature. Managers need to be aware that TMIIs are influenced by context, so that if a pattern such as a trophic cascade is observed the assumption is not immediately made that animal densities or structural changes have occurred in the food web.

# 1.9 Rothley and Dutton 2007 – in review

A greenhouse experiment was conducted using a spider-grasshopperresource system to explore the relative strength of trait and density effects, using lethal and non-lethal predators. We used a lab-type setting (as opposed to field) to avoid desiccation of foliage and facilitate tracing pre- and post-experiment vegetation. Our goals were to: 1) quantify the indirect effect of the non-lethal and lethal spiders on the plant resources, 2) compare the intensity of the trait effects generated by non-lethal and lethal spiders on the grasshoppers, and 3) evaluate the equivalence of our lab experiments to parallel research in the natural field setting.

Cages approximately 38cm tall were constructed from black Teflon® screen and plastic flowerpots, set up in rows in the greenhouse. Each cage contained vegetation consisting of grass, clover, and dandelion in a vial of water

to prevent desiccation. Each cage contained 4 grasshoppers. There were three forms of the predator treatment: 1) no predator, 2) a non-lethal predator, and 3) a lethal predator. Predators were rendered non-lethal by placing them inside a small (13 cm by 9 cm by 4 cm) aluminium screen cage inside the larger cage. We compared the grasshopper's diet choice, total food intake, and mortality in response to each of these treatments. We also contrasted the results of this lab experiment with those of field experiments on an analogous predator-prey-resource system. Discrepancies between the lab and field results were interpreted with respect to the experimental design in each setting and in terms of the predictions from the predation risk allocation hypothesis.

The reduction of total vegetation eaten associated with the *non-lethal* spiders (total TMII<sub>non-lethal</sub>) was the sum of the 'trait-mediated indirect interaction' (TMII<sub>non-lethal</sub>) which represents the grasshoppers eating less because they are afraid of the spiders and the 'trait-mediated mortality indirect interaction' (TMMII<sub>non-lethal</sub>) which represents the vegetation not eaten by grasshoppers that were scared to death by the spiders.

The reduction of total vegetation eaten associated with the *lethal* spiders (total TMII<sub>lethal</sub>/DMII<sub>lethal</sub>) was the sum of the 'trait-mediated indirect interaction' (TMII<sub>lethal</sub>) which represents the grasshoppers eating less because they are afraid of the spiders, the 'trait-mediated mortality indirect effect' (TMMII<sub>lethal</sub>) which represents the vegetation not eaten by grasshoppers that were scared to death by the spiders, and the 'density-mediated indirect effect' (DMII<sub>lethal</sub>) which represents the vegetation not consumed by grasshoppers that were eaten by the

spiders. The total TMII<sub>lethal</sub>/DMII<sub>lethal</sub> and TMII<sub>lethal</sub> were calculated similarly to total TMII<sub>non-lethal</sub> and TMII<sub>non-lethal</sub>, respectively. The average total TMII<sub>lethal</sub>/DMII<sub>lethal</sub> was 21.7% larger than the average total TMII<sub>non-lethal</sub>. The average TMII<sub>lethal</sub> was 149.7% larger than the average TMII<sub>non-lethal</sub>. The TMMII<sub>lethal</sub> and DMII<sub>lethal</sub> could not be separated because it was impossible to tell from the grasshopper carcasses which had been attacked and which died from being scared to death (Figure 8).

Per capita plant consumption rates of grasshoppers that survived the experiment were significantly higher in the absence of spiders versus lethal and non-lethal spiders present (P<0.01); however there was no significant difference in the amount of total vegetation eaten between cages with non-lethal (TMIIs) and lethal spiders (DMIIs). Average per capita intake was highest in the no spider cages (0.002555g), lower in the non-lethal spider cages (0.001675g), and lowest in the lethal-spider cages (0.001514g). Grasshoppers ate relatively little grass in the absence of spiders (17.9%), relatively more grass with non-lethal spiders (37.4%), and the most grass with lethal spiders (43.0%) (Figure 9). Note that these are likely to be overestimates of per capita intake, particularly in the cages with spiders, because the grasshoppers that died probably ate some of the vegetation in these cages before dying (i.e., the numerator in the per capita intake calculation should be larger).





Variation in consumption between spider treatments can also be attributed to a

temperature gradient along the length of the greenhouse. Separating the total

vegetation eaten into forbs and grasses, both the distance from the greenhouse

door and the spider treatment had a significant effect on forbs eaten

(P<sub>ANCOVA</sub><0.01, P<sub>door</sub>=0.01, P<sub>treatment</sub><0.01). Forbs eaten in both non-lethal spider

(P<0.01) and lethal-spider (P<0.01) cages was significantly different than in the no-spider cages but the difference between non-lethal spider and lethal spider cages was not significant (P=0.77). For grass eaten, distance to greenhouse door had a significant effect but the spider treatment was not significant ( $P_{ANCOVA}=0.22$ ,  $P_{door}=0.04$ ,  $P_{treatment}=0.88$ ) (Figure 10). The effect of the spider treatments on damage to individual plant species varied by species. The amount of clover and grass eaten decreased from no spiders to non-lethal spiders to lethal spiders. However, the amount of dandelion eaten decreased substantially from no spiders to non-lethal spiders but then increased for lethal spiders.



Figure 9. Average clover, dandelion, and grass eaten by grasshoppers in cages with no spiders, non-lethal spiders, and lethal spiders.



Figure 10. The results of the greenhouse experiments showing total vegetation eaten as a function of distance to the greenhouse door. The lines represent the least-squares regression between total vegetation eaten and distance to greenhouse door for grasshoppers with no spiders (solid line), grasshoppers in the presence of non-lethal spiders (short-dashed line), and grasshoppers in the presence of lethal spiders (long-dashed line). Circles, diamonds, and filled squares show the actual data from each cage in the no spiders, non-lethal spiders, and lethal spiders treatments, respectively.

Non-lethal spiders induced a significant, trait-mediated mortality

comparable to the density effect of lethal spiders that was not observed in the

field system. The number of grasshoppers alive at the end of the experiment was

significantly different between the no-spider and non-lethal spider cages (P=0.01)

and between the no-spider and lethal-spider cages (P=0.01), but not different

between non-lethal and lethal-spider cages. Grasshoppers in all treatments,

including the no-spider cages, experienced significant mortality. The average

number of grasshoppers alive in the no-spider cages at the end of the experiment was significantly lower than 4 (Figure 11).



Figure 11. Number of grasshoppers alive at the end of the greenhouse experiment in cages with no spiders, non-lethal spiders, and lethal spiders.

Further, damage to individual plant species by the grasshoppers appeared to reflect the particular spatial juxtaposition of the spiders and the plants imposed by our cage design. Experiments to explore predator-prey relationships frequently involve the artificial construction of predation risk conditions that vary in the degree to which they mimic any real-world system in their temporal and spatial pattern of risk, their physical environment, and the completeness of their ecological community. While providing a convenient and compelling means to test theory and discover the continuum of possible interactions between these organisms, as predicted from the predation risk allocation hypothesis, such experiments could yield unique results that do not transfer to a natural field setting. We conclude that were we to base our deductions on the results of the lab experiments, we would overestimate the consequence of the prey's risk response in the field.

Although we suggest caution when comparing lab and field-based experiments, there were some similarities in the results found in Rothley and Dutton (2006) found in the field; the proportional increase in grass intake as spiders grew "scarier" is consistent with the diet shift seen in that experiment, and certainly may have contributed to grasshopper mortality in cages with lethal and non-lethal spiders. Our results indicate that care must be given to the experimental design for predator/prey studies and caution used when extrapolating lab results to other settings.

# **CHAPTER 2: MANUSCRIPT**

# 2.1 Abstract

We conducted a greenhouse experiment to compare the relative contributions of trait-mediated indirect interactions (TMIIs) and density-mediated indirect interactions (DMIIs) to changes in density and resource usage in a threetrophic level predator-prey-resource system under varied shading conditions. The diet selections made by grasshoppers were measured in the presence and absence of caged and free-roaming spiders. Additionally, shaded and unshaded conditions were used to examine whether a change in environment alters the magnitude or relative contribution of trait-mediated and and density-mediated interactions (TMIIs and DMIIs, respectively). We show that there is a significant reduction in resource consumption due to TMIIs and DMIIs for all vegetation combined and in both shaded and unshaded conditions; specifically TMIIs are larger than DMIIs for forbs, while DMIIs are larger than TMIIs for grass. Total indirect interactions were nearly identical for shaded and unshaded conditions. Our results add to the growing literature suggesting that TMIIs are either as great or greater than DMIIs, and illustrate the difficulty of addressing how environmental change will affect interactions in complex plant and animal communities.

# 2.2 Introduction

Top-down effects by predators have been shown theoretically and empirically to have the potential to have an enormous influence on the density, structure, and diversity of organisms at lower trophic levels in a wide variety of ecosystems (Schmitz 1998, Werner and Peacor 2003, Ripple and Beschta 2004, Schlacher and Cronin 2006, Stief and Holker 2006). One version of this top-down predator influence is the density-mediated interaction (consumptive effect), where the predator kills and consumes prey, and the reduction in prey abundance can result in a density-mediated indirect interaction (DMII) between the predator and the prey's resource species (Schmitz et al. 2004, Werner and Peacor 2003). Such DMIIs could benefit all resources used by the prey if consumption were uniformly reduced, or decrease competition between the preferred and non-preferred resource species if the DMII were concentrated on the prey's preferred resource species. A second version of the top-down effect of a predator is the trait-mediated interaction (non-consumptive effect), where predation risk modifies the prey's behaviour, such as habitat or resource selection (Huang and Sih 1991, Peacor and Werner 1997), or life history (Abrams 1995), and results in trait-mediated indirect interactions (TMII) between the predator and the prey's resources. The dramatic consequences of DMIIs and TMIIs have been observed in natural systems and experimentally produced in both terrestrial and aquatic communities (Chase 1996, Beckerman et al. 1997, Schmitz 1998, Werner and Peacor 2003, Ripple and Beschta 2004).

Trait and density-mediated interactions and their associated indirect interactions are generally considered separate phenomena, but it is not unreasonable to assume that they can occur simultaneously to yield a combined density/trait-mediated top-down effect. For example, a predator may only consume a few or even one prey item, but its presence and activity are likely to induce risk response behaviour in the remaining live prey. While several studies have concluded that TMIIs are frequently either equal to or greater than DMIIs in magnitude (Wojdak and Luttbeg 2005, Pressier et al. 2005, Werner and Peacor 2003, Preisser et al. 2005, Werner and Peacor 2001, Huang and Sih 1991, Wissinger and McGrady 1993, Diehl et al. 2000), recent investigations have also noted that the relative importance of trait and density effects can vary, even for the same predator-prey-resource community, depending on context. Trussell et al. (2006) found that both the sign and the strength of DMIIs and TMIIs varied depending on whether they were measured in risky or refuge habitats. Wojdak and Luttbeg (2005) observed that whether TMIIs exceeded or were less than DMIIs depended on resource levels. If a predictive theory of the combined trait/density effects is to be developed, more research into the factors that control the relative importance of trait and density effects is required, particularly across real-life ecological and environmental gradients.

We designed a factorial experiment to examine the relative contribution of TMIIs and DMIIs in a predator-prey-resource system under altered environmental conditions. There is overwhelming evidence that human activities are modifying the spatial and temporal patterns of light and temperature at small and large

scales, and in urban, suburban, and remote settings (Kristan et al. 2003, Esseen and Renhorn 1998, Davies-Colley et al. 2000). These environmental modifications have been shown to alter the behaviour of plants and animals in the short term, frequently to their detriment in the long term. In the summer of 2005, we conducted a field experiments on a predator crab spider (family Philodromidae, genus Tibellus), its prey grasshopper (Melanoplus sanguinipes), and the grasshoppers' resource plants, and found that an alteration in light and temperature induced by shading could change the non-consumptive effect between the predators and prey and the TMII between the predators and the plants (Rothley and Dutton 2006). The experiments described here involved the same predator-prey-resource community, but were conducted in a greenhouse setting where we were able to control the types and abundance of resources presented to the grasshoppers and more precisely measure their food intake. Specifically, we wanted to answer the following questions: (1) Does shading change the combined density/trait indirect effect of the spiders on the plants? (2) Does shading change the occurrence or relative importance of TMIIs compared to the DMIIs? (3) Does the sign of the combined indirect density/trait effect of the predator on the resources vary between plant species and with shading?

The TMIIs between a top predator and resources via an intermediate prey species can be measured by comparing resource use by the prey in the absence of the predators versus in the presence of predators (that can be detected by the prey but cannot kill or consume prey) (Figure 12). This 'non-lethal' predator can be created by disabling the apparatus the predator uses to catch or kill prey

(Schmitz et al. 1998), or by a physical separation between the predator and the prey that maintains, to the extent possible, the chemical, visual, and/or audio cues used by the prey in predator detection (Bernot and Turner 2001, Peacor and Werner 1997). The combined DMII/TMIIs of the predator on the resource can be calculated by comparing resource use by the prey in the absence of the predators versus in the presence of a fully capable predator. Assuming the non-lethal predator is as 'scary' as the fully capable predator, the DMIIs can be estimated by comparing the prey's resource use in the presence of a non-lethal predator and



Figure 12. Assuming the non-lethal predator is as 'scary' as the fully capable predator, all additional reduction in food intake can be attributed to DMIIs. The combined TMII/DMII can be calculated by subtracting the fully-capable predator from the no predator treatment. However, the total reduction due to a fully capable predator is due to combined TMII and DMII (beyond the calculated DMII) that cannot be separated out.

subtracting out the TMII. This technique, however, has the potential to underestimate the DMIIs as it is impossible to know if magnitude of the TMII in the 'non-lethal' predator condition will be equivalent to the TMII in the capable predator condition. Conversely, the DMIIs will be overestimated if the non-lethal spiders are not as scary as the fully capable spiders.

## 2.3 Materials and Methods

We conducted our experiments during July 2006 in a 2 m by 3 m by 3 m greenhouse on Burnaby Mountain at Simon Fraser University, Burnaby, British Columbia, Canada. Temperatures in the greenhouse ranged from 22°C to 25°C during the course of the experiment, although we tried to keep the temperatures as constant as possible by opening or closing the greenhouse door. A total of 48 cages, 38 cm tall, were constructed from black Teflon® insect netting and plastic flower pots with a top diameter of 13 cm. The cages were assigned one of six treatments; 1) NO: no spider, unshaded; 2) CG: restrained spider, unshaded; 3) FREE: unrestrained spider, unshaded; 4) NOSHD: no spider, shaded; 5) CGSHD: restrained spider, shaded; 6) FREESHD: unrestrained spider, shaded. and set in a random, block design with the blocks arranged linearly at an increasing distance from the greenhouse door to account for the disruption the door opening/closing may have caused, and to parallel the temperature gradient measured across the greenhouse.

All grasshoppers, spiders, and plants were collected on Burnaby Mountain. Four second or third instar grasshoppers were placed in each of the

48 cages. We confirmed that these grasshoppers were small enough to be readily subdued and eaten by the spiders by feeding similar-sized grasshoppers to similar-sized spiders prior to initiating this experiment. Vegetation used in the experiment was clipped from the area immediately adjacent to the greenhouse, and consisted of grass and forbs, the forbs being made up of dandelion and clover. Enough was provided that it would not all be consumed within the duration of the experiment. Prior to the initiation of the experiment, three blades of grass (*Calamagrostis canadensis*), one dandelion leaf (*Taraxacum officinale*), and two clover leaves (*Trifolium repens*) were traced by hand onto paper, placed immediately in vials of water (to minimize desiccation), and set in a glass at the bottom of each cage. The tallest plant in each cage was typically the dandelion, followed by the grass, and then the clover.

All cages contained four second-instar grasshoppers and vegetation; cages with a spider present contained one spider. Depending on the treatment, spiders were either allowed to "free roam" in the cages (unrestrained) or they were placed in a separate rectangular (13 cm by 9 cm by 4 cm) cage made of aluminum screen, within the larger (38 cm) cylindrical cage. Cages assigned to the shaded treatment were wrapped with additional nylon screen (for a total of two layers of screen), such that light and temperature were reduced by 40% and 2°C, respectively. Unshaded cages had one layer of nylon screen.

The experiment ran for six days, after which all animals were returned to the field from which they were caught. Vegetation was re-traced onto the same preexperiment paper, so that the area of vegetation consumed during the

experiment could be calculated. This was done by scanning the tracing sheets and digitizing the images. The amount of vegetation consumed during the experiment was the post-experiment vegetation area subtracted from the preexperiment vegetation area.

The differences between treatment means in forb and grass consumption were compared using one-way analysis of variance (ANOVA). The number of grasshoppers alive at the end of the experiment and the amount eaten of grass, dandelion, clover, forbs (dandelion + clover), and total vegetation (grass + dandelion + clover) in shade and no shade were compared using an ANCOVA with the shade level as the treatment and relative distance from the greenhouse door as the covariate. Within shade treatments, the number of grasshoppers alive at the end of the experiment and the amount eaten of grass, dandelion, clover, forbs, and total vegetation were compared using an ANCOVA with the predator type (none, caged, free-roaming) as the treatment and relative distance from the greenhouse door as the covariate. The difference in the means between predator treatments was considered to be significant if the difference between their least squared means exceeded the Tukey HSD criterion value at alpha=0.05.

The effect of the shading on the grasshoppers without spiders was tested by comparing the number of grasshoppers alive at the end of the experiment and the amounts eaten of grass, dandelion, clover, forbs, and total vegetation in shade and no shade using an ANCOVA with the shade level as the treatment and relative distance from the greenhouse door (greenhouse temperature

gradient) as the covariate. The spider treatment and greenhouse temperature gradient effects on grasshopper mortality and the amounts eaten of grass, dandelion, clover, forbs, and total vegetation in shaded and unshaded cages were tested using an ANCOVA with the spider type (none, caged, lethal) as the treatment and relative distance from the greenhouse door as the covariate. Comparisons between the spider treatments were made with *a priori* Least Squared means contrast tests.

## 2.4 Results

The magnitudes of the TMII and DMII effects in the presence of spiders can be thought of as the change in consumption of vegetation, compared to consumption in the absence of predators. Thus, -0.60 corresponds to a 60% reduction in consumption of the indicated resource type for the given treatment. Numbers that are negative mean that food intake was reduced, while positive numbers indicate an increase in consumption. Trait-mediated indirect interaction corresponds to the change in consumption due to the presence of a caged spider, while DMII corresponds to the reduction in consumption due to a freeroaming spider. Total indirect interaction is the combined TMII and DMII.

There was no significant difference between the size of effect within any of the vegetation types (forbs or grass). There was also no significant difference between TMII or DMII between shading types. In the unshaded cages there was no significant difference between TMIIs and DMIIs; in the shaded cages TMIIs were larger than DMIIs by a marginally insignificant amount (P=0.06).

Total indirect interaction effects (TII) were of approximately the same magnitude in the shaded and unshaded conditions (Table 2 and Figure 13). Looking at grass, the DMII effects were larger than the TMII effects in both shaded and unshaded conditions (but not significantly). The reduction in foraging for grass due to TMIIs and DMIIs was greater in shaded conditions compared to unshaded (Figure 14) (not significant). The opposite holds for TMII and DMII effects for forbs, where reductions in consumption due to TMIIs are larger than DMIIs (Figure 15).

In the cages with no spiders, there was no significant difference between shaded (n=8) and unshaded (n=8) cages and no effect of distance from the greenhouse door on the number of grasshoppers alive at the end of the experiment ( $P_{ANCOVA}=0.56$ ,  $P_{treatment}=0.30$ ,  $P_{door}=0.87$ ), or on the amount eaten of dandelion ( $P_{ANCOVA}=0.44$ ,  $P_{treatment}=0.40$ ,  $P_{door}=0.34$ ) eaten. In cages with no spiders, shading had no significant effect on the amount of grass, clover, or forbs eaten but there was a significant decrease in the amount grass ( $P_{ANCOVA}=0.04$ ,  $P_{treatment}=0.75$ ,  $P_{door}=0.01$ ), clover ( $P_{ANCOVA}=0.06$ ,  $P_{treatment}=0.17$   $P_{door}=0.04$ ), forbs ( $P_{ANCOVA}=0.06$ ,  $P_{treatment}=0.12$ ,  $P_{door}=0.05$ ), and total vegetation ( $P_{ANCOVA}=0.02$ ,  $P_{treatment}=0.16$ ,  $P_{door}=0.01$ ) eaten with increasing greenhouse temperature.

Table 2.Mean differences in effect size for trait-mediated indirect interactions (TMII),<br/>density-mediated indirect interactions (DMII) and total indirect interaction (TII),<br/>for vegetation types under shaded and unshaded conditions. The asterisk (\*)<br/>denotes which effect is larger, TMII or DMII.

	TMII	DMII	TII	
Shaded	-0.5906*	-0.0944	-0.6292	All vegetation
Unshaded	-0.5756*	-0.0973	-0.6169	
Shaded	-0.2975	-0.3457*	-0.5403	Grass
Unshaded				
	-0.0239	-0.1817*	-0.2013	
Shaded	-0.6812*	0.1658	-0.6667	Forbs
Unshaded	-0.7019*	-0.0340	-0.7120	



Figure 13. Change in consumption of total vegetation under different shading conditions for TMII, DMII, and TII, from left to right.



Figure 14. Change in consumption of grass under different shading conditions for TMII, DMII, and TII, from left to right.



Figure 15. Change in consumption of forbs under different shading conditions for TMII, DMII, and TII, from left to right.

In the non-shade cages, there was a significant difference in the total vegetation eaten between spider treatments and as a function of distance from the greenhouse door (P<sub>ANCOVA</sub><0.01, P<sub>treatment</sub><0.01, P<sub>door</sub><0.01). Total vegetation eaten in the no-predator cages (n=8) was significantly higher than both the caged-spider (n=7; P<0.01) and lethal spider cages (n=8; P<0.01), but there was no difference between total vegetation eaten in caged-spider and lethal spider cages (P=0.56). In the shade, there was no significant effect of the spider treatment or the distance from the greenhouse door. Considering just forbs, in the no-shade condition total vegetation eaten between spider treatments and distance from the greenhouse door were still both significant (PANCOVA<0.01, P<sub>ANCOVA</sub><0.01, P<sub>door</sub><0.01), and total forbs eaten in the no-predator cages was significantly higher than both the caged-spider and free-roaming spider cages. Looking at each plant species alone, there was a significant difference in the dandelion eaten between spider treatments but distance from the greenhouse door was marginally significant (P<sub>ANCOVA</sub>=0.49, P<sub>treatment</sub>=0.04, P<sub>door</sub>=0.07). Dandelion eaten in the no-predator cages was significantly higher than with the free-roaming spiders (P<0.01) and with the caged spiders (P<0.01). There was a significant effect of distance from the greenhouse door on clover eaten while the spider treatment was marginally insignificant (PANCOVA<0.01, Ptreatment=0.06,  $P_{door} < 0.01$ ). Grass consumption was significantly correlated with distance from the greenhouse door but there was no significant effect of the spider treatments (P<sub>ANCOVA</sub>=0.14, P<sub>treatment</sub>=0.78, P<sub>door</sub>=0.03) (Figure 16).



Figure 16. The total amount of vegetation eaten as a function of the distance from the greenhouse door by spider treatment in shaded (top) and unshaded (bottom) cages.

#### 2.5 Discussion

In the absence of predators, the grasshoppers had no foraging or density response to the shading treatment. Their response to the shading treatment in the presence of the spiders therefore must have resulted from a change in their interaction with the spiders caused by the shading. In the absence of predators, the grasshoppers did, however, eat less the farther they were from the greenhouse door. Assuming increasing distance from the greenhouse door is a surrogate for rising temperature, the grasshoppers' decreased food intake, and associated activity time, matches the observed field pattern where grasshoppers reduce their activity levels during the warmer parts of the day. This may be the result of thermal stress or perhaps of anticipation that spider predators are more active with warmer temperatures.

Although the differences in magnitude between TMIIs and DMIIs are not significant between shading conditions or between vegetation types, there was a significant reduction in total vegetation consumption due to TMIIs and DMIIs in both shaded and unshaded conditions. This is consistent with the recent findings of Werner and Peacor (2001), Huang and Sih (1991), and Wissinger and McGrady (1993), all of whom found TMIIs to be either as large or larger than DMIIs.

One pattern shown by the data is that TMII effects are stronger than DMII effects for forbs, while the opposite is true for grass. This may be because dandelion (which represented a larger proportion than clover of forb mass in the cages) was up higher in the cages, closer to where the restrained (non-lethal)

spider was, which might have discouraged the grasshopper from eating it. For grass, it may be that the grasshoppers are unperturbed by restrained spiders because the grass is at a lower vertical position than the dandelion, but when the spider is allowed to roam free, then predation (density effects) reduces the grass consumption.

In one treatment, FREESHD (free-roaming spiders in shaded cages), grasshoppers consumed *more* forbs on average compared to NOSHD (no spiders present in shaded cages). Although the difference was not significant, this seems unusual and is consistent with Rothley and Dutton (2006), who found the same result in a field study. This could be due to the grasshoppers using the dandelion as a vantage point for better observing the free-roaming spider or a avenue to escape attack, resulting in incidental foraging; observing the animals during the experiment might help provide an answer. While the direction of effect found in this study almost all contributes to a reduction in consumption (negative), it may be possible for DMIIs and TMIIs to have effects in opposite directions (Dill et al. 2003). For instance, the FREESHD treatment has a positive DMII effect, the CGSHD treatment has a negative TMII effect, and the overall TII is negative.

In shaded cages, we found significantly higher grasshopper mortality when the spider was free-roaming (66%) versus when the spider was absent (31%), but not between restrained (50%) and absent. In unshaded cages, Rothley and Dutton (2007 – in review) found significantly higher grasshopper mortality when the spider was free-roaming (59%) *and* restrained (57%), than

when the spider was absent (19%). Because there were no significant differences in diet between shaded and unshaded cages and yet grasshopper mortality was higher in free-roaming and restrained unshaded cages, it suggests the trait-mediated mortality may be due to spiders appearing "scarier". This is consistent with Rothley and Dutton (2006), who suggested that spiders may be perceived as "scarier" by grasshoppers under conditions with higher light. It also suggests a kind of chronic predation effect whereby the grasshopper may not obtain crucial nutrients due to heightened awareness of the spider's presence in high light conditions; previous studies have shown that a sustained high grass diet can lead to increased or total mortality (Beckerman et al. 1997). How an animal would perish due to a persistent predation risk is difficult to imagine; because the cages were not continuously observed we do not know what behaviours were exhibited by the grasshoppers in the cages with restrained spiders. A future experiment that removed the possibility of a cage effect in favour of a more natural situation would be beneficial in determining whether the cage design and structure played a role in grasshopper mortality.

The results of this study have several implications for the management of natural systems. The magnitude of TMIIs and DMIIs is greater for grass under shaded conditions, while for forbs TMIIs are greater in unshaded conditions whereas DMIIs are greater in shaded conditions. This indicates that a varying environmental context may alter the magnitudes of indirect effects and overall total effect; the ways in which species in the same food web interact thus may change as environmental cues are altered (Orrock et al. 2004). From a

management perspective, this is important because changing interactions between predators and prey can filter throughout the food web and impact species that are several times removed from the interacting trophic levels (Dill et al. 2003, Werner and Peacor 2003). Preisser et al. (2005) found in their metaanalysis of TMIIs and DMIIs that while density effects attenuated through food chains, TMIIs remained strong. Managers of complex ecosystems cannot safely assume that observed changes in abundance of a particular species is due to a density effect, and must be sufficiently aware of the biology and behaviour of the species to know whether changing environmental conditions might be causing TMIIs, or altering their relative impact.

# **CHAPTER 3: DISCUSSION**

# 3.1 Implications for Wildlife Management

The above described three experimental outcomes show that abiotic changes impact the ways that animals in the same food web interact, potentially altering community structure. In Rothley and Dutton (2006), we showed that elevating light and temperature resulted in a classic trophic cascade pattern; we postulated that grasshoppers changed their diet in response to increased awareness of predation risk. In Rothley and Dutton (2007 – in review), we demonstrated that non-lethal predators can have as large an effect as those that are lethal, and suggested that non-natural settings may influence estimates of TMII and DMII impacts. In manuscript 3 we showed that the abiotic effect of shading can change the magnitude of TMIIs and DMIIs, and that TMIIs can have as large an effect or larger than DMIIs.

What does this mean for management of parks and protected areas, where wildlife managers are entrusted to protect species diversity? Recently there has been a push to integrate into wildlife and conservation management knowledge from other scientific disciplines such as behavioural biology (Singh and Kaumanns 2005), behavioural ecology (Anthony and Blumstein 2000), physiology (Wikelski and Cooke 2006, Carey 2005, Block 2005), human sociology and recreation (Fernandez-Juricic et al. 2005, Daley et al. 2004).

Integration of other disciplines can add "tools" to the managers' toolbox by raising awareness of all options available to manage wildlife.

Managers of parks and protected areas have typically responded to changes in observed food web dynamics by examining *density effects* such as interference competition and predation (Karieva 1994), and the fact that TMIIs do not yet have a clear role in management models and paradigms may make it difficult to convey the importance of abiotic impacts. However, as Bolker et al. (2003) point out, there is anecdotal evidence from long-term and large-scale studies that TMIIs may affect community dynamics at practical management scales. This study argues that managers need to be aware of three things:

1) interactions in food webs occur in several ways, via consumptive effects, DMIIs, non-consumptive effects, and TMIIs;

2) the amount of time an organism allocates to performing certain behaviours will change the magnitude and frequency of consumptive and nonconsumptive effects and TMIIs and DMIIs, and;

3) the disturbances that may cause organisms to shift their behaviour can be either physical or abiotic.

Each of the above is expanded upon below, with tables to help managers recognize changes in interactions and potential disturbances, respectively.

Additionally, limitations to this study are explored, along with ideas for future directions for how to further elucidate how abiotic changes alter plant and animal communities.

#### 3.1.1 Understanding the Foodweb

Being aware of the importance of TMIIs and DMIIs and their potentially changing influence under different abiotic conditions is not meant to be an additional burden on the manager. Rather, it should be thought of as another item in the toolbox that can be considered when thinking about how to best manage wildlife. Recognizing a change in foodweb interactions means having a good understanding of the plant and animal community so that perturbations can be recognized. Effective managers should possess a good knowledge of the trophic components that make up the foodweb, the species that make up each trophic level, the flow of energy between trophic levels, and present and historical foodweb structure. Managers should ask themselves "are the components here that should be here?" "Are there certain predators or other species that are absent?" "Are there certain species (such as top predators) whose potential change in behaviour or impacts on the food web might be more important than others?" Table 3 gives a list of things to know about the target foodweb to better understand it.

The reintroduction of wolves in Yellowstone National Park is a good example of how understanding non-consumptive effect s and TMIIs enabled managers to recognize the importance of having a top predator present. The extirpation of the wolves allowed the elk population to explode and reduced the heterogeneity of woody browse species. Culling the elk proved a temporary solution; when stopped, the numbers shot up again, a clear indication that the ecosystem was somehow out of balance. Not only was the elk population

reduced (a consumptive effect), but other trophic levels benefited from the TMIIs associated with wolf reintroduction. Woody browse recovered, demonstrating a classic trophic cascade. Had park managers understood earlier the influence of TMIIs and put less attention on holding populations to a certain number, the situation might have been remedied earlier.

The presence of a certain trophic component in a system does not necessarily indicate ecosystem health or likely persistence of those organisms currently present. All may appear well to a manager who is tracking species presence and abundance, but numbers may not tell the whole story. Predator avoidance can reduce prey population growth, as prey shift to less suitable microhabitats (Schmitz 1998, Downes 2001), reduce foraging (Morrison 1999) or mating effort (Ryan et al. 1981), or redirect resources from reproduction to chemical or structural defenses (Barry 1994, Bolnick and Preisser 2005). Thus, while the numbers of animals may appear satisfactory, non-consumptive effects and TMIIs can depress their growth and population health. A manager aware of this might not select culling as a first choice to reduce predators when a prey species falls in numbers. Although culling can provide a short-term solution to reduce non-consumptive effects and adverse impacts on a prey population, once the culling ceases and the predator population rebounds the prey population will be subject to the same non-consumptive effect and TMII effects. Even before non-consumptive effects and TMIIs possibly manifest themselves in the form of reduced population growth, a manager knowledgeable in the structure of the foodweb can identify potential impacts abiotic changes and conjecture what

	Understanding the Food Web
1	Identification of trophic levels and number of trophic levels
2	Identification of species that make up trophic levels
3	Knowledge of energy flow between trophic levels
4	Current and historical food web structure

Table 3. Understanding food web structure.

impacts it might have on the animal population, taking preventative measures where possible (see Section 3.1.2 Knowing the Behaviour of Organisms, below).

Being aware of non-consumptive effects and TMIIs may help managers see the "bigger picture", where interactions other than those where organisms come into direct contact are considered, and trophic levels several times removed from a focal species are also considered. Being conscious of densitymediated interactions is relatively easy because it is obvious when an organism kills or consumes another. Because non-consumptive effects and indirect interactions are difficult to observe with the naked eye and are less obvious than consumptive effects, finding an indicator species within the study system will help managers gauge changes in species interactions. In our experiments we used a resource that could be measured over time. Finding vegetation that is easily observable or an animal population whose numbers can be an indicator of overall food web interactions would be beneficial.

Population numbers may yet remain the best way to assess whether parks and protected areas are meeting their goals and objectives. After all, while there are many criteria by which a protected area can be judged, it cannot be considered successful if target populations cannot be sustained. If non-

consumptive effects and TMIIs do in fact play a significant role in species interactions by depressing a species' birthrate, health, diet, fecundity, etc., it will be manifested in the form of a reduced population. However, the drawback to thinking solely about population numbers (and ignoring the possibility of nonconsumptive effects and TMIIs) is that it may take a while to manifest itself if generation times are long.

#### 3.1.2 Knowing the Behaviour of Organisms

Once managers understand the structure of their study system, they can better appreciate the ways that certain behaviours might impact the overall community structure. We were able to design and conduct experiments because we knew the biology of our study system. Insects were used as study organisms because spiders and grasshoppers use vision (Bailey and Harris 1991, Heiling et al. 2005) and are sensitive to temperature fluctuations (they are cold blooded); it was appropriate to manipulate these abiotic factors in our experiments. Additionally, we understood the sort of trade-offs each organism would be making and it allowed us to interpret the results of our experiments in the context of predation risk. A manager that deals with warm blooded animals would have to take different factors into consideration. For instance, smell may be more important to target species; in that case focus should be on how chemical or pheremonal cues might influence interactions. Human produced pollution or formerly sequestered chemicals volatilized by global warming could potentially disrupt olfaction.

Managers must be acutely aware of the ways in which individual species in their care might respond to abiotic changes; more specifically they need to think about the way that organisms might *differentially* respond and the trade-offs they might make. Knowing which resources and what geographic areas are used, and temporal-spatial movement patterns can help a manager identify perturbations. If prev are being forced into other habitat or to use a different resource, it may be an indication that predation risk has changed (Heithaus and Dill 2006, Mao et al. 2005, Chase 1996, Wojdak and Luttbeg 2005) due to some kind of disturbance. Recall that in seeking refuge from potential predators, foods encountered may be highly dissimilar compared to preferred habitat, in their nutritional quality, required handling times, and edibility (Schmitz 1994), which can impact fitness. Imagine a food web where, due to changed temperature cues, insects emerge earlier and birds migrate later. This new abiotic context skews temporally the way these two organisms would usually interact, with one species shifting forward in time, the other later. The insects, unencumbered by their normal predators, can freely feed on their resource (vegetation), causing more damage than normal. By the time the birds arrive at their destination, the insects may have matured and mostly perished. Now, the birds need to find a new food source. They may shift their attention to another insect, creating a new set of consumptive and non-consumptive effects, TMIIs and DMIIs that previously were absent, which in turn may affect resources in the food web. Although this example highlights temporal shifts and our experiments dealt with "fixed" trophic structures (that is, all trophic components were present during the

entire experiment), it is nonetheless critical that managers think about how the organisms in their care might be temporally affected by abiotic changes.

Instead of surveying animal and resource abundances (that is, the components of the food web) to rectify changes in food web dynamics that are considered negative, managers may need to look elsewhere. Disturbances need not directly affect the components of a food web in any way; they may even occur outside the area of management and still have dramatic effects on food web dynamics. Additionally, an observed decline in a particular species does not mean that that species needs to be the target of restoration efforts. If in fact a species is negatively affected due to disturbances occurring many "links up the chain," restoration efforts focused on that species may prove ineffective and wasteful of both time and money. Managers must understand that trophic cascades can be caused by physical and non-physical factors. If they observe it, they have to think about these two "pathways."

# 3.1.3 Identifying Abiotic Threats to Parks and Protected Areas

If managers understand how the behaviour of their target species can influence community dynamics, and they know how those species might differentially react to the same disturbance, it will allow them to more easily recognize potential disturbances (Table 4).

Development may occur outside, near the border, of a park or protected area (that is, there is no structural change to the habitat) but still have an impact. Light gradients from developments can often "reach" into the protected area,

even if development is located outside the boundary. Miller (2006) found that elevated light levels from light pollution caused American Robins to begin their songs earlier in the morning. As noted earlier, photoperiod is important for the development of many species (Dolezal and Sehnal 2007, Berrill et al. 2006). It is now believed that encroaching development is one of the top threats to parks in North America (Stottlemyer 1987, Soden 1991). Atmospheric and waterborne pollution from development may also pose a threat. Kozlowski and Vass-Bowen (1996) suggest including a buffer zone in all planning around parks and protected areas to mitigate against these external threats, and others have suggested managers use existing law in an effort to control what kind of development goes on near park borders (Bader 1999).

Results of this project's research may also have implications for how animal species are protected if it is shown that direct effects on animals or their resources need not be present to alter food web dynamics; currently, under the Endangered Species Act (U.S.) and the Species at Risk Act (Canada) only destruction of species and their habitat is explicitly prohibited. It begs the question of exactly how and who to punish when abiotic factors negatively influence community dynamics. Some cases are easier to address than others – laws exist to punish polluters where culpability is clearly demonstrated. But what about light and temperature, for instance? Can a company be held accountable for emitting too much light, if the ultimate outcome is detrimental to a species?

A major looming (literally and figuratively) question is how climate change might affect wildlife. A whole suite of abiotic changes may potentially accompany
climate change in addition to well documented Increases in temperature (global warming) (Dunn and Winkler 1999, Kiritani 2006). Temperature increase has been linked to declines in amphibian populations (Pounds el al. 2006). Light-level fluctuations due to changing albedo (Gibbard et al. 2005) make this study particularly relevant.

Elevated temperatures have the potential to liberate chemicals formerly sequestered in snow and ice, making them subject to long range atmospheric transfer processes (Valle et al. 2007). Additionally, as snowpack melts formerly sequestered chemicals may become volatile and undergo atmospheric transference; there is speculation that continued global warming will allow populations to become more mobile (Valle et al. 2007). Additionally, as the climate warms, there is a trend for lake temperatures to rise (DeStasio et al. 1996, Schindler et al. 1990). Salmon streams that receive snow melt may see an increase in chemicals that alter temperature signatures that the salmon depend on for feeding cues (Henderson et al. 1992). Elevated temperatures will likely also lead to higher concentrations of sodium and chloride, as well as toxins, due to longer water retention times (Schindler 1997).

Impact types/ Changes to environment		Disturbance
Physical	Structural	Habitat fragmentation, destruction
	Density	Population density change in predator or prey
Abiotic	Chemical	Volatilization of sequestered molecules
	Pollution	Air, water
	Light	Human development, climate change, creation of edge
	Temperature	Climate change, creation of edge

Table 4. Summary table of disturbance types.

Returning to parks and protected areas, the animals within protected areas will respond physiologically to changes in climate. Although elevated temperatures will likely lead eventually to shifts in vegetation (Burns et al. 2003) and resulting range shifts for animals, this structural vegetation change may be preceded by physiological responses in the animals that feed on said vegetation. The result is one of two outcomes: the organism remains in its current range to feed on optimal food sources, but at a physiological and metabolic suboptimal temperature; or, the organism shifts its range in response to a new temperature gradient, feeding on suboptimal resources at a metabolic and physiological optimal temperature. The second scenario has received attention recently, as U.S. and Canadian parks services have addressed a need for more flexible park boundaries, citing the Yellowstone to Yukon corridor as an example that would allow organisms to shift their range within a protected zone (Raimer and Ford 2005).

Another component of climate change is increasing UV levels due to changing albedo and reflectivity (McKenzie et al. 2007, Zepp et al. 2007). Heling

et al. (2007) demonstrated that the crab spider *Thomisus spectabilis* (predator) attracts honeybees (prey) to flowers (resource) by reflecting UV (UV+). Being UV reflective also has a drawback, however: it's an attractant to blue tits, which eat *T. spectabilis*. When *T. spectabilis* was sprayed with Parasol® to make them UV absorptive (UV-), the spiders ceased to attract honeybees, and were less visible to their predator, the blue tit. Thus, it is easy to imagine how changes in UV might alter the way organisms interact with each other when the perception of one or more species in the food web depends on abiotic factors that are subject to fluctuation.

This brings up a final point regarding climate change – if we care about how we are influencing our environment, we must reduce anthropogenic factors contributing to global warming. The insidious nature of global warming goes hand in hand with TMIIs – not because TMIIs are inherently bad, but because the effects of each can be difficult to visualize. In the same way that managers must change the way they think about food web interactions to include the nonphysical so that they are more aware of non-consumptive effects and TMIIs, the general population needs to consider the creeping changes that global warming will bring to bear both to our "human" world and the natural world we entrust ourselves to protect.

## 3.2 Limitations to this Study

One of the most obvious perceived limitations of this research is the study system. Grasshoppers and spiders are not the kind of sexy or charismatic species that the public might consider important, and it is valid to wonder if insect

species are really important at all or relevant to managers. The study system in this case is a model system only, where the focus is not on the species *per se* but rather on testing of ideas using the subject species. That said, insects are often an important part of ecosystems that managers must consider. One only has to look at current events regarding mountain pine beetle infestations, the spread of which has been linked to climate change (Campbell et al. 2007). While the study system we examined only contained arthropod animals and plants, insects are an important trophic level in many ecosystems, as a source of food for vertebrates (Finke and Winn 2004) and as a consumer of resources (Harper 1966, Girma et al. 2006, Veteli et al. 2006).

As Schmitz (2005) points out, although management in the real world is carried out over vast and heterogeneous landscapes, the key is to have a good conceptual understanding of ecosystem function and structure. Schmitz (2005) suggests the ecological principle of foraging versus predation risk avoidance trade-offs as "one central organizing conceptualization for plant-herbivore interactions across all systems." Again, it is apparent how important it is for a manager to know their organisms intimately; one must understand what behaviours are potentially being traded off for another to know how it might affect the food web. We feel the study system we used is fundamentally the same as any other food web, no matter how large the organisms may be.

Additionally, this research only examines three trophic levels in a food web that no doubt involves many more organisms; *Tibellus* may be preyed upon by birds or mice, while the grasses and forbs involved likely depend on soil micro-

organisms. Due to limitations of time and scope, however, examining a threetrophic-level system was the only feasible option. Additionally, this study makes the point that a changed abiotic context can alter behaviours in species that can lead to community alteration. Most of the examples presented here from the literature only make concrete connections between a single abiotic factor and a single species. How exactly TMIIs and DMIIs will change depending on species, and whether that change will be predictable is not easy to answer. Relyea and Yurewicz (2002) point out that while it might be possible to successfully predict the magnitude of TMIIs and DMIIs in a three trophic level system based on pairwise experiments, any added complexity may make it very difficult. Again, this is why managers must have intimate knowledge of how different trophic levels interact.

## 3.3 Future directions

Although we were able to answer the big-picture question of "Are traitmediated behavioural responses to disturbance, alone, enough to change food web dynamics?" in our experiments, we were unable to determine the relative effects of light and temperature separately on either spiders or grasshoppers. Such an experiment would determine whether trait-mediated responses from the *M. sanguinipes* and *Tibellus* are species-specific. Cages with demarcated quadrants could be placed in varying light and temperature conditions, and cameras could record the movement of both spiders and grasshoppers inside the cages. Distance travelled, number of strikes (of spiders against grasshoppers),

and time spent sedentary would be recorded to determine whether increases in light and increases in temperature differentially affect either anima's beahviourl.

Of note, but not discussed specifically in this document (as it is a structural change), is the ways in which climate change will influence vegetation growth and thus shift habitable ranges for animals. Burns et al. (2003) suggest that U.S. national parks are likely to lose up to 20% of their biodiversity if mammalian species relocate due to shifts in vegetation under doubled CO2. It would be interesting to see how plant leaves and overall health respond to elevated light, temperature, and CO2. Does the plant as a resource become less appealing to grasshoppers? Do grasshoppers prefer plants that have been exposed to certain abiotic conditions?

## 3.4 Conclusion

Awareness of abiotic factors, non-consumptive effects, and TMIIs will encourage managers to think more holistically regarding their system of interest. Although TMIIs as yet do not have a clear role in management models and paradigms this study argues that managers need to be aware that interactions in food webs occur in several ways, via consumptive and non-consumptive effects, DMIIs and TMIIs, that the amount of time an organism allocates to performing certain behaviours will change the magnitude and frequency of TMIIs and DMIIs, and that disturbances that may cause organisms to shift their behaviour can be either physical or abiotic.

The study system used for this study is a simple tri-trophic system, but in the real world non-consumptive effects, TMIIs and DMIIs may be more difficult to measure and identify. Disturbances are more complex and can be made up of smaller disturbance components, each of which may affect animals in a different way. Similarly, foodweb structure, animal behaviour, and disturbances are all presented in separate sections above, but in reality, knowledge of any one will help in understanding the others.

Quantification of TMIIs and DMIIs is not an easy thing to do, and there is no one right way to do it. However, for managers to effectively argue that nonconsumptive effects and TMIIs are important in their systems of interest, they will have to demonstrate how community interactions are being altered. In the same vein, abiotic factors that are not necessarily inherently disruptive (such as light and temperature) will have to be convincingly shown to have negative impacts if policy makers are going to take abiotic changes seriously. The need for accurate community models incorporating non-consumptive effects and TMIIs will require closer collaborations between theory and experiment in an effort to successfully predict how interactions can be altered by disturbance at higher trophic levels.

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