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Adaptive foraging behaviour and impact on longevity of an omnivorous insect in response to the extreme temperature fluctuation events associated with climate change

Jessica Sparkes

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ADAPTIVE FORAGING BEHAVIOUR AND IMPACT ON LONGEVITY OF AN
OMNIVOROUS INSECT IN RESPONSE TO THE EXTREME TEMPERATURE
FLUCTUATION EVENTS ASSOCIATED WITH CLIMATE CHANGE

by

Jessica Sparkes

A Thesis
Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2012

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ABSTRACT

One expected consequence of global climate change is an increased likelihood in extreme weather events, including higher amplitude temperature fluctuation. This work examined the effect of low and high amplitude temperature fluctuation on predation, foraging behaviour and longevity of *Dicyphus hesperus* Knight (Heteroptera: Miridae). Results indicate that temperature fluctuations do influence foraging behaviour and adult longevity but the degree to which these are influenced is affected by host plant species. The results from this work suggest that the role of temperature fluctuation should be considered in future research as constant temperature models may not be representative of what is currently occurring in nature (low amplitude fluctuations) or what may occur as a result of climate change (high amplitude fluctuations).

*To my parents, for their endless support and encouragement
and for always believing in me.*

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CHAPTER 1 : INTRODUCTION AND LITERATURE REVIEW

General Introduction

Global climate change is a major phenomenon affecting all aspects of our environment. Since 1940, the mean global temperature has increased by 0.8°C (Solomon 2007). Furthermore, by 2040 it is predicted that the mean temperature of midwestern North America will increase by 1.5-3.5°C (Pan *et al.* 2004). Global climate change will affect every organism on the planet and as poikilotherms, insects are particularly vulnerable to these changing temperatures. Over the past few decades, entomologists have investigated the impact of climate change on arthropod fauna, focusing on the effects of global warming, CO₂ enrichment, and changes in precipitation levels. Throughout the literature, one aspect of global climate change that is largely overlooked is the effect of fluctuating temperatures. In their 2007 report, the Intergovernmental Panel on Climate Change (IPCC) reported that along with the increase in mean temperature there will likely be an increase in temperature variance, leading to more frequent and more intense heat waves (Solomon 2007). Modeling research suggests that increases in temperature variability (both frequency and amplitude) will have significant effects on predation dynamics of animals, especially those which are poikilothermic (Logan and Wolesensky 2007). Possible consequences of the change in predation dynamics include extinction or outbreaks. This research examines the effects of both high and low amplitude temperature fluctuations on the foraging behaviour of an omnivorous insect species.

Literature Review

Global climate change

Most people agree that one of the biggest global issues at the present time is climate change. The mean global surface temperature has risen by nearly 0.8°C since 1850 (Solomon 2007) and according to the NASA Goddard Institute for Space Studies, the fourteen warmest years in the past century have all occurred in the last two decades (<http://data.giss.nasa.gov/gistemp/> 2007). Global warming is not the only aspect of climate change that we are experiencing. Extreme weather events have started occurring more frequently and have been more intense throughout the last 50 years (Meehl and Tebaldi 2004, Solomon 2007). Heavy precipitation, drought, extremely high sea levels, heat waves, and temperature fluctuations are all examples (Meehl and Tebaldi 2004, Solomon 2007).

Climate change is occurring in a large part, due to increased levels of greenhouse gases. The greenhouse gas effect refers to the presence of water vapour, ozone, aerosols, and most notably, carbon dioxide, within the earth's atmosphere (Wang *et al.* 1976), creating a blanketing effect. Thermal radiation enters the atmosphere, reflects off the earth's surface and rather than exiting the atmosphere, is re-radiated, thus causing an increase in the earth's temperature. The greater the amount of greenhouse gases in the atmosphere, the greater the effects of climate change. This accumulation of greenhouse gases occurs naturally and also because of human activity. The dramatic increase in the rate which the climate has changed in the last 40 years can largely be attributed to human activity. Since 1970, greenhouse gas emissions as a result of human activity have risen by 70% (Solomon 2007). Over half of the anthropogenic gas emissions are the result of carbon dioxide from the use of fossil fuels in energy production (Solomon 2007). Anthropogenic gas emissions are considered to be the likely cause of extreme weather events (Solomon 2007).

It is predicted that the global mean temperature will continue to rise and that the frequency and intensity of extreme weather events, including heavy precipitation, drought, heat waves and temperature fluctuations will also continue to increase. The rate at which this increase will occur is dependent upon the level of anthropogenic greenhouse gas emissions in the future. The IPCC suggests that greenhouse gas emissions at or above the current level will likely result in changes in the next century to be more severe than what we have experienced in the past century (Solomon 2007). According to their 2007 report, the IPCC predicts that the mean global temperature will increase by between 1.8-4.0°C in the 21st century.

Climate has various effects on each individual species and thus, on entire ecosystems (Andrewartha and Birch 1954). Temperature, precipitation, carbon dioxide levels, and wind patterns, as well as other climatic factors, all directly affect organisms (see references within Burns (1999) and Ansu and McCarney (2008)). In addition to the direct effects of climate, organisms are also influenced by climate indirectly through the climatic effects on their habitat or food sources (McCarty 2001). As the climate changes, each organism responds to the changes in different ways and as a result, ecosystems are in a constant state of change (Committee on Ecological Impacts of Climate Change 2008). Although the constant changes that ecosystems are experiencing are not a new occurrence, it is now happening at a more rapid pace. Changes in climate can result in changes to individual species phenology, physiology and distribution patterns as well as changes to species composition, and overall function of ecosystems. Burns (1999) and Ansu and McCarney (2008) have compiled bibliographies of experimental studies documenting the effect of climate change on individual species as well as ecosystems. In addition to changes within ecosystems, research shows that climate change was likely the

driving force in recent species extinctions (McLaughlin *et al.* 2002) and invasive outbreaks (Dukes and Mooney 1999). Furthermore, this trend is highly likely to continue (Thomas *et al.* 2004). The IPCC reports that of all plants and animal species studied thus far, between 20-30% are likely to be at a greater risk of extinction should the global mean temperature increase more than 2.5°C (Solomon 2007).

Insects and climate change

All organisms are impacted by climate change. However, poikilothermic animals, such as insects, are influenced significantly more than others. Temperature directly influences the speed of metabolism in insects (Andrewartha and Birch 1954). This, in turn, will affect developmental rate, movement, predation rate and oviposition rate (Gilbert and Raworth 1996). Development varies along a temperature curve and each individual species is unique with its temperature requirements. As temperature increases, towards an upper threshold, all aspects of development time tend to decrease. Egg development, emergence time and nymphal development are decreased and therefore, stage progression increases and adult longevity is reduced (Gullan and Cranston 2005). As a result of the reduced nymphal period, reproduction periods are increased and population doubling times are decreased (Gullan and Cranston 2005, Logan *et al.* 2006). Increased temperatures also tend to increase the movement activity of insects. Increasing activity can lead to an increase in encounter rates (Speight *et al.* 1999, Elliott *et al.* 2000, Rott and Ponsonby 2000, Khan 2010) and a decrease in handling time (Dreisig 1981, Gilbert and Raworth 1996, Mohagheh and Tirry 2001, Khan 2010, Sentis *et al.* 2012) of predators whilst increasing escape capabilities of prey (Dreisig 1981, Schmalhofer and Casey 1999). Predation rate also changes as temperature increases. This change is

somewhat more complex as it involves the interaction of two or more organisms that are affected by the temperature increase individually. As stated, both predator and prey respond to an increase in temperature with increased activity, thus predation rate can increase, decrease or remain unchanged depending on the relative effect of the temperature on the predator and prey (Kruse *et al.* 2008). Usually, the predator's foraging ability increases at a greater rate than the prey's escape ability, therefore increasing predation rate (Skirvin *et al.* 1997, Perdikis *et al.* 1999, Kruse *et al.* 2008, Korenko *et al.* 2010). The effect of temperature on predator-prey interaction strength of ladybeetles and aphids has been examined through models and laboratory experimentation (Sentis *et al.* 2012). Results of this study indicate that in periods of extreme temperature (i.e. above the upper threshold), predator searching decreases and that predation rate is non-linear, depending firstly on searching rate and secondly on handling time, and will decrease when temperatures approach thermal limits. Once the temperature reaches an upper threshold, development is halted, reproduction fails and if exposure lasts long enough then the insect will eventually die (Andrewartha and Birch 1954, Danks 1987). Reasons for this shut down are not entirely known. Early research indicated some possibilities such as: inadequate oxygen intake (Buddenbock and Rohr 1922), accumulation of acid waste as a product of metabolic processes (Fraenkel and Herford 1940, Lamb 1961), and increased water loss as a result of structural changes to the lipids in the cuticle (Gunn 1933, Beament 1961). More recently, it is assumed that extreme high temperatures cause cell death as a result of denatured proteins and altered enzyme and membrane structure and function (Korsloot *et al.* 2004, Gullan and Cranston 2005). An accumulation of denatured proteins triggers the production of heat shock

proteins, thus inhibiting protein synthesis (Korsloot *et al.* 2004, Gullan and Cranston 2005).

Poikilothermic organisms in general, and small insects, more specifically are expected to respond more quickly to fluctuations in temperature than other organisms because of how quickly their bodies react to the external temperatures. Insects respond quickly to changes in temperature because of their high surface to volume ratios which allows for quick gas exchange (May 1985). In a natural environment, temperature typically undergoes regular diurnal fluctuation and as such, there exists a wealth of research on the effects of daily fluctuating temperatures on insect development. Unfortunately, the literature is full of conflicting reports. Research indicates that diurnal temperature fluctuation can have a positive effect, a negative effect, or no effect on the development of various insect species (Behrens *et al.* 1983). Furthermore, it is unclear whether the differences in development under diurnal temperature fluctuation are due to the temperature fluctuations or the influence of light-dark phase.

Little data exist on the effect of temperature fluctuation on predation. Saleh *et al.* (2003) studied the effect of high constant and alternating temperatures on the prey consumption of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae). In their study, *Aphis gossypii* Glover (Homoptera: Aphididae) consumption by adult *D. tamaninii* was higher at 30°C constant temperature than at either alternating temperature of 25/15°C or 35/22°C and lowest at 35°C constant temperature, which ultimately resulted in death (Saleh *et al.* 2003). This suggests that although a fluctuating temperature may not encourage an increase in predation over a constant temperature, it may extend the temperature range at which an insect can function. Insects exposed to fluctuating temperatures have higher optimal and upper developmental thresholds (Davis *et al.* 2006). Logan and Wolessensky

(2007) predict long term effects of more frequent temperature fluctuations on predator-prey populations with standard functional response models. This study suggests that increased amplitude in temperature fluctuations will lead to decreases or possible extinctions in prey populations (Logan and Wolessensky 2007). Bannerman *et al.* (2011) examined the effect of fluctuating temperature on aphid-parasitoid interactions and found that when trait-mediated parasitoid disturbances were isolated from the direct effects of foraging, an increase in both frequency and amplitude of extreme temperatures had a significant effect on aphid populations but when the direct effects of foraging were included there was no effect of temperature on foraging ability.

Omnivory

An omnivore, in its broadest sense, is defined as a consumer that feeds on resources from multiple trophic levels (Pimm and Lawton 1978). Omnivory is a very common and widespread feeding strategy among insects (Polis *et al.* 1989, Whitman *et al.* 1994, Alomar and Wiedenmann 1996, Polis and Winemiller 1996). Research shows that over 40 insect families from 12 different orders include at least one omnivorous insect species (Coll and Guershon 2002). Due to the large number of trophic interactions that an omnivore experiences, the concept of omnivory in food webs is quite complex (Arim and Marquet 2004). Historically, it was thought that the presence of omnivory would destabilize food webs and should, therefore, be rare in nature (Pimm and Lawton 1978, Pimm 1982). Now, we know that this is not the case. Throughout the 1990s, several researchers demonstrated that omnivory was not rare at all, but rather, should be considered the norm in any food web (Diehl 1993, Polis and Winemiller 1996, McCann

and Hastings 1997). Omnivory has been shown to locally stabilize, as well as, enhance persistence in food webs (McCann and Hastings 1997).

In 2002, Coll and Guershon specified the definition of omnivory. They defined a “true” omnivore as a specific case of trophic omnivory in which a consumer feeds on both plant and animal tissues (Coll and Guershon 2002). Further mention of omnivory will refer to this specified definition. For an omnivore to be able to consume both plant and prey materials, they require specific morphological and physiological adaptations. Examples of these adaptations include; specialized digestive tracts, mouthparts, and the secretion of specific digestive enzymes (Eubanks *et al.* 2003).

Omnivore Feeding Strategies

Omnivores fall into one of three categories; opportunistic, obligatory, and facultative (Coll and Guershon 2002). Obligate omnivores require the consumption of both plant and prey materials to survive. *Dicyphus hesperus* Knight (Heteroptera: Miridae) is an example of an obligate omnivore. *Dicyphus hesperus* requires the water obtained from plant feeding to digest any prey that it may consume via extra-oral digestion (Gillespie and McGregor 2000). A facultative omnivore supplements its primarily herbaceous or carnivorous diet with prey or plant material respectively, to increase its overall fitness. Examples of this include some thrips, such as western flower thrips, which normally consume plant material, but may feed on the eggs of spider mites, a competitor (Agrawal *et al.* 1999) or, a primarily carnivorous mantid, *Tenodera aridifolia sinensis* (Saussure), which has been found to have increased fitness when supplementing its diet with plant pollen (Beckman and Hurd 2003).

Omnivores feed on a vast array of food types and as such, it is challenging for researchers to unravel their complex feeding strategies. Optimal foraging theory states that organisms forage in a way that maximizes the energy gained and minimizes the cost associated (MacArthur and Pianka 1966). In the case of some omnivores, feeding on both plant and prey material in combination is required for success. In this situation the insect must allot the appropriate amount of time and energy to the intake of each, in order to maximize overall fitness. Theory dictates that if resources are equivalent, then feeding will commence on whichever resource is encountered (Fryxell and Lundberg 1994). However, this is rarely ever the case and the omnivore must adopt some form of adaptive foraging strategy (Holt and Polis 1997, Krivan and Diehl 2005). The omnivore has the choice of feeding on the more abundant resource, plant material, which tends to be less nutritious or searching for prey, which can be more nutritious but is less abundant and requires more time and energy output. We must also take into account that the two resources are not independent of each other, since the search for prey usually results in the omnivore finding a location of suitable plant material (Coll 1996). Nutritional value varies between each individual food source. Individual prey quality varies with size, age and health of a particular insect. Research shows that prey quality increases with its position in a food web, suggesting that a predator is of higher quality than an herbivore (Hastings and Conrad 1979, Whitman *et al.* 1994, Hairston 1997, Elser *et al.* 2000, Denno and Fagan 2003). To assess overall prey quality however, we must consider population size, mobility and defense strategies of the prey communities. Plant quality also varies. Each suitable host plant has specific morphological, nutritional and phytochemical traits that influence the omnivores feeding decision (Coll 1996, Coll and Guershon 2002).

Biological control

Biological control is defined as the human introduction or enhancement of natural enemies of pest species in an attempt to restore a balance (Gullan and Cranston 2005). These natural enemies are biological control agents and can be any predator, parasitoid or pathogen that can potentially influence the pest's abundance and/or dynamics (Coppel and Mertins 1977, Bugg *et al.* 1987, Pickett and Bugg 1998). For effective utilization of a biological control agent, there must be a solid understanding of its foraging behaviour (DeBach and Rosen 1991). Historically, it was believed that the best practice of biological control was the classical application which introduces specialist natural enemies, with the hope that they become permanently established (Gullan and Cranston 2005). The use of generalist predators as biological control agents was once thought to be a poor choice, more recently however, they have become a common and successful method, especially in temporary agroecosystems (Symondson *et al.* 2002). Generalist predators may be better suited as biological control agents because they are able to persist through times of target prey scarcity by feeding on alternative prey (Bugg *et al.* 1987, Eubanks and Denno 1999, Symondson *et al.* 2002). Predatory Heteroptera have received a lot of attention as important and useful biological control agents (Coll and Ruberson 1998).

It is essential for success, that a biological control agent is able to function in the environmental conditions present in its ecosystem. Furthermore, since the goal of biological control is to suppress prey populations, it is important that the biological control agent being used is achieving an adequate level of predation under the given environmental conditions.

Model system

Dicyphus hesperus, used in this research as a model for generalist predators, is a mirid bug, native to North America, which feeds on a variety of plant and insect species (Gillespie and McGregor 2000, McGregor and Gillespie 2005, Shipp and Wang 2006). Throughout the past decade, research has been conducted to evaluate *D. hesperus* as a potential biological control agent of various pests. McGregor *et al.* (1999) pointed out that numerous species of predatory Miridae from the subfamily Bryocorinae and the tribe Dicyphini have been successfully used for the biological control of various pests throughout Europe yet up until that time no research had been conducted on North American predatory Miridae. At the conclusion of their study, McGregor *et al.* (1999) determined that *D. hesperus* showed potential as a North American version of various European biological control agents and thus, research on this particular species followed.

Dicyphus hesperus is an excellent choice as a model system for many reasons: it is widely distributed throughout North America (Kelton 1980, Henry and Wheeler 1988); a large body of research exists on many aspects of this particular species (McGregor *et al.* 1999, Gillespie and McGregor 2000, McGregor *et al.* 2000, Sanchez *et al.* 2002, Sanchez *et al.* 2003, VanLaerhoven *et al.* 2003, Gillespie and Sanchez 2004, McGregor and Gillespie 2004, Sanchez *et al.* 2004, Sinia *et al.* 2004, Gillespie and Quiring 2005, McGregor and Gillespie 2005, Roitberg *et al.* 2005, Laycock *et al.* 2006, Shipp and Wang 2006, VanLaerhoven *et al.* 2006, Alma *et al.* 2007, Bennett *et al.* 2009a, Bennett *et al.* 2009b, Ma *et al.* 2009), and there is a practical application of *D. hesperus* as a biological control agent (McGregor *et al.* 1999), as well as numerous closely related species that are used around the world for biological control.

Dicyphus hesperus are considered to be obligate omnivores as they typically require both plant and prey material for survival and reproduction (Gillespie and McGregor 2000). It was once assumed that plant feeding occurred only when prey was limited (facultative switching behavior) (Alomar and Albajes 1996, Cohen 1996, Naranjo and Gibson 1996, Coll and Ruberson 1998, Agrawal *et al.* 1999); however, research with *D. hesperus* has shown an alternate feeding scenario. Firstly, when plant feeding occurs as a supplement to prey feeding, there is an increase in life history traits. In this situation, the plant feeding is adding a level of nutrient that prey cannot provide. Secondly, plant feeding is essential to the organism as it enables prey feeding (Gillespie and McGregor 2000). It is proposed that plant feeding by *D. hesperus* provides the water that is necessary for the extra-oral digestion (Cohen 1995) of prey material or perhaps that the water is required to maintain osmotic balance (Gillespie and McGregor 2000). Extra-oral digestion is a form of food preparation (Kaspari 1990) used by predatory Heteroptera (Cohen 1995). The process of extra-oral digestion involves injecting an item of prey with digestive enzymes, which allows the predator to then suck up the liquefied content. Extra-oral digestion allows predators to feed on prey much larger than they would otherwise be able to handle (Cohen 1990, 1995, Cohen and Tang 1997) but does come at the cost of constant water loss.

Research has also indicated that *D. hesperus* tends to move and feed more at night (VanLaerhoven *et al.* 2003). This behaviour has also been shown in the similar species, *M. pygmaeus* (Perdikis *et al.* 1999, 2004). Sanchez *et al.* (2004) demonstrated that *D. hesperus* showed a preference for certain plants and that the nutrition gained from plant feeding varied among plants. Mullein (*Verbascum thapsus* L., Scrophulariaceae) is the only known food source that is able to solely support *D. hesperus* throughout its entire

life cycle and allow for reproduction (Sanchez *et al.* 2004). In the presence of prey, *D. hesperus* was able to complete development on all plant species tested. However, development time varied significantly (Sanchez *et al.* 2004).

Predation studies have been carried out to assess how other mirid bugs respond to various temperature conditions. As previously stated, *D. tamaninii* has been found to consume more aphids at a constant temperature of 30°C than either one of two fluctuating temperature regimes (Saleh and Sengonca 2003). Perdakis *et al.* (2004) studied the predation of *M. pygmaeus* at various temperatures and found that predation rate of adults when feeding on aphids was highest at 30°C. This study did not include any fluctuating temperatures, but did compare predation on two plant species and three photoperiods and found that predation rate varied between the two plant species. This difference in predation rate was greater at the warmest temperature of 30°C (Perdakis *et al.* 2004).

Hypotheses

The present work examines the effect of temperature fluctuation on predation and longevity of *D. hesperus*. Chapter two compares predation rate and the likelihood that a predation event will occur during each period of a day. This experiment also examines the effect of plant species and its interaction with temperature fluctuation. The hypothesis was that temperature fluctuation and plant type would affect predation. The prediction was that predation would be least likely to occur during periods of high temperature (in both high and low amplitude fluctuation) and that this would be particularly evident when *D. hesperus* was able to prey feed on high quality plants (mullein).

Chapter three delves deeper into the effects of temperature fluctuation on *D. hesperus* predation, observing the behaviour of the insects at several times within the

fluctuation. Based on the results obtained in chapter two, the hypothesis was that temperature fluctuation caused the predation behaviour of *D. hesperus* to change. The prediction was that during periods of peak temperature, predation would slow or stop entirely but to compensate for this, there would be a sharp increase in predation during other times in the day. It was also predicted that warm temperatures (within the optimal temperature range) would decrease walking/searching time, yet increase encounter rate, and decrease handling time and that low temperatures would cause the reverse.

Chapter four examines the effect of temperature fluctuation on *D. hesperus* adult longevity. The hypothesis was that adult longevity would be affected by temperature fluctuation. However, the prediction was that this would only be the case with the high amplitude fluctuation which would increase early mortality.

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**CHAPTER 2 : THE INFLUENCE OF TEMPERATURE FLUCTUATION AND
PLANT TYPE ON *DICYPHUS HESPERUS* KNIGHT (HETEROPTERA:
MIRIDAE) PREDATION**

Introduction

Global climate change is occurring. The mean surface air temperature is expected to rise by 1.4-5.8°C by 2080 (Solomon 2007). Along with this severe increase in mean temperature, it is also expected that temperature variation will become more frequent and more severe (Meehl and Tebaldi 2004, Solomon 2007). Insects are particularly vulnerable to climate change because they are poikilotherms and their biological functions are proportionate to the external temperatures (Gullan and Cranston 2005). Small insects in particular, have a high surface area to volume ratio relative to larger organisms, making their response to temperature fluctuation very rapid (May 1985).

Predation rates are affected both directly and indirectly by temperature. Low temperatures slow development and therefore, increase the duration of each stage of development. This can result in a greater level of stage-based predation (Logan *et al.* 2006). High temperatures increase movement and thus, can increase encounter rates and decrease handling time of predators whilst also increasing the escape capabilities of prey. Many studies have demonstrated that the overall effect of increasing temperature (up to a threshold level) is an increase in predation rate (Perdikis *et al.* 1999, Mahdian *et al.* 2006, Kruse *et al.* 2008, Simonsen *et al.* 2009, Jalali *et al.* 2010). This implies that the increased encounter rate of the predator is more important than the increased escape capability of the prey. Beyond an upper threshold however, predation decreases (Mahdian *et al.* 2006). Other studies show the opposite relationship (Kruse *et al.* 2008). Sentis *et al.* (2012) examined the effect of temperature on predator-prey interaction strength using models and laboratory experiments with ladybeetles and aphids. They found that although handling time decreases exponentially with increased temperature,

search rate follows a hump-shaped pattern illustrating that predator searching decreases at extreme temperatures. The authors show that the effect of temperature can be nonlinear and that predation rate can decrease as thermal limits are reached. They suggest that predation rate, in relation to temperature thresholds, is determined primarily by searching activity and secondly by handling time.

However, it's not simply the mean temperature that is important in determining predation. Because activity is often determined by daily temperature fluctuation, changes to this fluctuation may cause either the predator or the prey to become more or less active (Logan *et al.* 2006). Due to their fast response to changing temperatures, insects are likely to vary instantaneous predation rate with temperature. The predation of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) was greater at a constant temperature of 30°C than at fluctuating temperatures of 25/15°C or 33/22°C but lowest at constant 35°C, which ultimately resulted in death of the predator (Saleh and Sengonca 2003). This particular result suggests that the constant temperature of 35°C was above the temperature threshold for this particular species; however, it has been shown that fluctuating temperatures can increase the threshold limits of insects (Davis *et al.* 2006). Another study examined the effect of high amplitude temperature fluctuation (as a simulated heat wave) on aphid populations in the presence of parasitoids and found that aphid numbers were not affected in the presence of a single parasitoid species but were affected by the heat wave when two parasitoid species are in competition (Gillespie *et al.* 2011).

Dicyphus hesperus Knight (Heteroptera: Miridae) is a generalist omnivore with applications as a biological control agent for greenhouse whitefly, two-spotted spider mite and western flower thrips in greenhouse tomato crops (McGregor *et al.* 1999, Shipp and Wang 2006). *Dicyphus hesperus* is native to North America and is widely distributed

throughout (Kelton 1980, Henry and Wheeler 1988). Studies by VanLaerhoven *et al.* (2003) demonstrated that *D. hesperus* is more active and has a higher predation rate during the night hours. This nocturnal behaviour was also observed by Perdikis *et al.* (1999, 2004) with *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae), a member of the same tribe. *Macrolophus pygmaeus* consumed more prey in the dark than in the light and this effect was amplified at higher temperatures (Perdikis *et al.* 2004). Perdikis *et al.* (2004) also found that the propensity for *M. pygmaeus* to feed more in the dark was greater on pepper plants than on eggplants.

Studies by Sanchez *et al.* (2004) show that *D. hesperus* females show preferences for certain host plants. This study also demonstrated that development time, fecundity, and longevity were all influenced by host plant but in various ways (Sanchez *et al.* 2004). It is unclear what specific attributes the preferred plants possess. Mullein was the only plant included in the study in which *D. hesperus* was able to reproduce in the absence of additional prey. Research has also demonstrated that the presence of mullein in a tomato greenhouse improves the ability of *D. hesperus* to establish (Sanchez *et al.* 2003). In spite of the establishment benefits of preferred plant, it is unknown what effect plant type has on *D. hesperus* predation. Research on western flower thrips (*Frankliniella occidentalis*) has shown that omnivores have a higher predation rate while on low quality plants than while on high quality plants (Agrawal *et al.* 1999, Agrawal and Klein 2000, Magalhães *et al.* 2005), possibly to compensate for the lower level of nutrients obtained from the low quality plant.

The objective of the present work was to determine if two different temperature fluctuations had an effect on the total number of prey consumed by *D. hesperus* over a five day period and also, to determine if the temperature fluctuations had an effect on the

likelihood of predation occurring during different times of day and on different host plants. The hypothesis was that temperature fluctuation and plant type would affect predation. The prediction was that predation would be least likely to occur during periods of high temperature (in both high and low amplitude fluctuation) and that this would be particularly evident when *D. hesperus* was able to prey feed on high quality plants (mullein).

Materials and Methods

Insect rearing

Laboratory colonies were established using *D. hesperus* that was originally captured from white stem hedge nettle (*Stachys alben* A. Gray (Lamiaceae)) near Woody, California USA (35°42'15"N, 118°50'00"W) at an elevation of ca. 500 m. These colonies were maintained at 25 ± 1°C, 50% RH and 16:8 L: D photoperiod. *Dicyphus hesperus* were reared on tobacco *Nicotiana tabacum* L. (Solanaceae) and fed previously frozen *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs *ad libitum*. Eggs were obtained from Beneficial Insectary Inc., Guelph, ON, Canada.

Plants

Four plant species were used in this study. Tomato (*Lycopersicon esculentum* Mill. cv. Rhapsody (Solanaceae)), pepper (*Capsicum annuum* L. cv. Bellboy (Solanaceae)), eggplant (*Solanum melongena* L. cv. Black Beauty (Solanaceae)), and mullein (*Verbascum thapsus* L. (Scrophulariaceae)). Tomato, pepper, and eggplant plants were grown hydroponically in rockwool growing medium. Mullein plants were grown in soil. All plants were grown in a greenhouse at the Agriculture and Agri-Food Canada Greenhouse and Processing Crops Research Centre in Harrow, Ontario, Canada

Temperature Regimes

Trials were conducted in controlled environment chambers set to various climatic conditions. Three temperature regimes were used to study the effects of temperature fluctuations on *D. hesperus*. The first was a constant temperature of 23°C. This temperature was selected as the control as it is well within what is considered optimal temperature of *D. hesperus* (Gillespie and Sanchez 2004). The second temperature regime simulates mean temperatures of south western United States in the summer months (Data obtained from the Western Regional Climate Centre), where the population of *D. hesperus* used for these studies was originally obtained. The 24 hour mean temperature is 23°C but the daytime (maximum) temperature is 32°C and the night (minimum) temperature is 17°C (Figure 2.1). The third temperature regime simulates an extreme weather event. Once again, the 24 hour mean temperature was kept at 23°C but in this model, the daytime (maximum) temperature reached 39°C and the night (minimum) temperature fell to 17°C (Figure 2.1). All three regimes were set to the same photoperiod of 16:8 (L: D). Relative humidity was chosen with vapor pressure deficit (VPD) in mind. Due to the practical greenhouse applications of these studies, the VPD was selected based on what would be appropriate for the greenhouse production of the specific plant species (Ontario Ministry of Food and Agriculture 2009). VPD was maintained between 0.70 – 2.17 kPa. In accordance with this, the relative humidity of all temperature regimes fluctuated with the temperature. The relative humidity of treatment one, with the constant temperature was set at 75%. The relative humidity of treatment two, the low amplitude fluctuation ranged from 69-85%. The relative humidity of treatment three, the high amplitude fluctuation ranged from 69-90%.

Experimental Protocol

Leaf segments were used in the experiment: 35 mm² segments were cut from healthy leaves to include the mid rib as well as multiple veins. Leaf disks were placed in prepared Agar gel in 90 mm diameter plastic Petri dishes. One week old adult female *D. hesperus* were removed from the colony, separated into individual containers and prey starved for 72 hours. During the last 24 hours, the *D. hesperus* were moved into their experimental arenas. Each Petri dish received a single insect. A full factorial experimental design was used, including the four plant species as well as a no plant control and three temperature regimes. In total, 15 treatments were examined, each with 11 replicates. At the end of the 72 hour starvation period, *E. kuehniella* eggs were presented to the *D. hesperus* as the prey item. The *E. kuehniella* eggs were presented on the sticky side of a 5 mm² piece of Post-It© note (3M) (approximately 75-100 eggs, well in excess of what could be consumed in the timeframe). The *E. kuehniella* was replenished every eight hours for a period of five days. Once the post-it was removed from the treatment, the number of prey consumed was counted by examining the deflated egg casings. Results were then transformed to represent one of two results: predation occurring (more than 5 eggs were consumed) or predation not occurring (5 or fewer eggs were consumed).

Statistical Analysis

Predation likelihood results were analysed using generalized estimating equations followed by pairwise comparisons with a Bonferroni adjustment. Generalized estimating equations is an extension of the general linear model which allows for the analysis of data containing repeated measures or other correlated data (Zeger and Liang 1986). Total

number of prey consumed over the five day period was analysed using Kruskal-Wallis ANOVA on ranks.

Results

Temperature regimes

A total of 45 *D. hesperus* died during the experiment and were excluded from the analysis (Table 2.1). Total prey consumption did not vary among the temperature regimes ($\chi^2=4.162$, $df=2$, $p<0.125$), nor did the likelihood of a predation event occurring (Wald $\chi^2=0.924$, $df=2$, $p=0.630$) (Table 2.2). Temperature regime and time frame interacted to affect the likelihood of predation occurring (Wald $\chi^2=9.599$, $df=2$, $p=0.048$) but the effect is not uniform across all plant types and time frames (Figure 2.2). In the constant temperature regime, the likelihood of predation occurring is different between 2100-500 h and 500-1300 h (posthoc pairwise comparisons: $p=0.033$), but both of these time frames are equal to 1300-2100 h ($p>0.05$). The likelihood of predation occurring in the low amplitude fluctuation is equal across all time frames ($p>0.05$). The likelihood of predation occurring in the high amplitude fluctuation is equal for 2100-0500 h and 1300-2100 h ($p>0.05$), but different between 0500-1300 and 1300-2100 h ($p=0.013$) and 2100-0500 and 0500-1300 h ($p=0.003$).

Plant type

Plant type affected the likelihood of a predation event occurring (Wald $\chi^2=14.165$, $df=4$, $p=0.007$) and the cumulative number of *E. kuehniella* eggs consumed over the five days (Kruskal Wallis $\chi^2=79.064$, $df=4$, $p<0.001$) (Table 2.3). Regardless of temperature regime or time of day, *D. hesperus* had the greatest likelihood of prey feeding while on

eggplant or mullein host plants, followed by tomato; and the lowest likelihood of prey feeding was while on pepper plants or in absence of a host plant (Figure 2.3).

The interaction between temperature regime, time frame and plant type has a significant effect on the likelihood of predation (Wald $\chi^2=39.306$, $df= 16$, $p<0.001$) (Figure 2.4). This interaction is difficult to interpret as there are no clear trends in where the differences in likelihood of predation lie. Within the high amplitude fluctuation, likelihood of predation was greater between 2100-500h than 500-1300h by a significant ($p<0.05$) margin in mullein and tomato and although not significant, the trend was the same in eggplant and pepper. Within the constant temperature regime and the low amplitude fluctuation there is no difference in likelihood of predation at certain time periods on any plant except mullein and eggplant, respectively. In the no plant treatment, none of these trends are evident.

Discussion

Regardless of plant type or time frame, the temperature regime did not affect the likelihood of predation occurring or the total number of prey consumed during the experiment. All treatments maintained the 24 hour mean temperature. Therefore any effect observed would have been of the fluctuation and not of a change in cumulative degrees. This was different than the study by Saleh and Sengonca (2003) who found that an insect from the same genus, *D. tamaninii*, consumed more prey when subject to a constant temperature then when subjected to fluctuating temperatures. In the experiments conducted by Saleh and Sengonca (2003), the mean temperatures were not equal across temperature regimes.

The interaction between temperature regime and time had a significant effect however; much of what was expected was not observed. Time frames were chosen to represent specific periods in the day; 2100-0500h represented overnight, 0500-1300h represented the morning and 1300-2100h represented the afternoon. Previous studies by VanLaerhoven *et al.* (2003) show that *D. hesperus* have a higher predation rate during the night compared to daylight hours. A breakdown of each of the time frames in each temperature regime of this study indicate that this is only true in the constant temperature, where prey feeding is most likely overnight, followed by the afternoon, and least likely in the morning, and in the high amplitude temperature fluctuation, where prey feeding in the overnight period is more likely than the morning but equal to that of the afternoon. This information suggests that in a natural situation *D. hesperus* does not necessarily feed more during the night but rather, that if conditions are varied in either direction (increasing or decreasing the amplitude of fluctuation), the feeding pattern shifts. When comparing all time frames in each of the temperature regimes, prey feeding was most likely overnight in the high amplitude fluctuation. A study comparing predation rates at different temperatures under different light-dark phases found that *M. pygmaeus* also had a higher predation rate during the overnight period, but that this result was much more pronounced in higher temperatures (Perdikis *et al.* 1999, 2004). Although this study was done using only constant temperatures, the results may be linked. The propensity to feed more during the night in warmer temperatures (both constant and fluctuating) may be a response to the adverse climatic conditions. In this study however, overnight periods were cool and it is possible that the increased likelihood to prey in the evening was offset by the drop in temperature. Perdikis *et al.* (2004) also note that the relationship between higher temperatures and increased overnight feeding is different between host plants

pepper and eggplant. This observation was also true of the present work. *Dicyphus hesperus* was more likely to prey feed overnight on mullein or pepper plants when subjected to the high amplitude temperature fluctuation. This result is interesting because the two plants are so different. Mullein is a preferred plant to *D. hesperus* while pepper is not. The physical structure of the two plants are also very different, mullein is much heartier and is rather hairy, while pepper leaves are completely smooth. Perdakis *et al.* (2004) suggest several possible explanations for the difference in predation between the two plant species. One explanation is the different microclimates on the leaf surfaces, caused by different levels of transpiration in each plant species.

Examination of the low amplitude fluctuation results shows a general trend that on high quality plants (mullein and eggplant) predation likelihood is greatest during the afternoon and lowest overnight. This result follows what was expected based on the insects feeding behaviour changing as the temperature changes. As discussed earlier, predation tends to increase as temperature increases (up to a threshold). However this was not the case with the lower quality plants (tomato, pepper, and no plant). Examination of the results in the high amplitude fluctuation reveal very different trends which suggests that the peak temperature is beyond the upper threshold, allowing them to survive but not function properly. Studies dealing with aphids at extreme high temperatures and temperature fluctuations with high maximums reveal that fluctuations typically extend the outer thresholds of aphids, allowing them to function across a greater range of temperatures (Messenger 1964, Davis *et al.* 2006). At 35°C, 64% of *D. hesperus* nymphs died before completing development (Gillespie and Sanchez 2004), as such, we can assume that 39°C is beyond the upper threshold. Therefore, *D. hesperus* responds similarly to aphids with regards to high amplitude fluctuating temperatures, that is,

increasing upper threshold levels. Results do however suggest that although the periods of extreme high heat do not kill the insects, they do cause a shift in predation behaviour. Further examination of the predation behaviour during this time is necessary to determine what effect the high amplitude fluctuation is having on the predation of *D. hesperus*.

Results show that *D. hesperus* has a greater likelihood of predation as well as a greater total consumption of *Ephestia* eggs when on eggplant or mullein hosts. This result is consistent with nymphal performance data obtained for *D. hesperus* by Sanchez *et al.* (2004), which showed mullein to be one of the most preferred host plants, and pepper to be one of the least preferred. Eggplant was not included in the Sanchez *et al.* 2004 study. Based on the present results, eggplant seems to be a suitable host plant for *D. hesperus*. High predation numbers on eggplant coupled with the low variability in feeding times across all temperature regimes suggest that *D. hesperus* could be an effective biological control agent for eggplant pests. In contrast, the high variability in feeding times observed by *D. hesperus* on mullein (a natural host plant) suggest that increases to the amplitude of temperature fluctuations, as a result of climate change, may have significant effects on the predation behaviour of this species. Although the total number of prey consumed by *D. hesperus* did not change as a result of the various temperature fluctuations, timing of the feeding did. Changes in temperature are an important consideration to be made in the study of predator-prey interactions (Logan *et al.* 2006). The present study uses a prey source that is essentially unaffected by the climatic conditions to focus attention on the effect on the predator. In a natural system this would not be the case and predator-prey dynamics would be influenced by the changes to all species involved. Nonetheless, the results indicate that changes to amplitude in temperature fluctuation will impact the feeding pattern of this species and

thus, further work is required into the effects of daily temperature fluctuations on the dynamics of predation.

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Tables

Table 2.1: Number of *D. hesperus* that died during the experiment and were therefore excluded from the analysis.

Temperature regime	Plant	Excluded due to mortality	N
Constant temperature	Eggplant	1	10
	Mullein	2	9
	No Plant	7	4
	Pepper	2	9
	Tomato	1	10
Low amplitude fluctuation	Eggplant	1	10
	Mullein	1	10
	No Plant	9	2
	Pepper	5	6
	Tomato	1	10
High amplitude fluctuation	Eggplant	1	10
	Mullein	0	11
	No Plant	7	4
	Pepper	2	9
	Tomato	6	5

Table 2.2: Total prey consumption and likelihood of a predation event occurring in each temperature regime (plant and time frame pooled). Means followed by the same letter are not statistically significant ($p > 0.05$).

Temperature Regime	Total prey consumption (mean \pm SE)	Likelihood of a predation event occurring (mean \pm SE)
Constant (n=40)	132.00 \pm 1.79 ^a	0.491 \pm 0.0184 ^A
High amplitude (n=42)	137.36 \pm 1.68 ^a	0.514 \pm 0.0184 ^A
Low amplitude (n=38)	135.04 \pm 1.80 ^a	0.499 \pm 0.0195 ^A

Table 2.3: Results of Generalized Estimating Equations (GEE) modeling the likelihood of *D. hesperus* preying on *E. kuehniella* eggs while exposed to various temperature regimes and plant types.

Factor	Wald Chi-Squared	Degrees of freedom	Significance
Temperature Regime	0.924	2	0.630
Time	6.717	2	0.035*
Plant type	14.165	4	0.007*
Temperature regime*Time	9.599	4	0.048*
Temperature regime*Plant	8.303	8	0.404
Plant*Time	12.583	8	0.127
Temperature regime*Time*Plant	39.306	16	0.001*

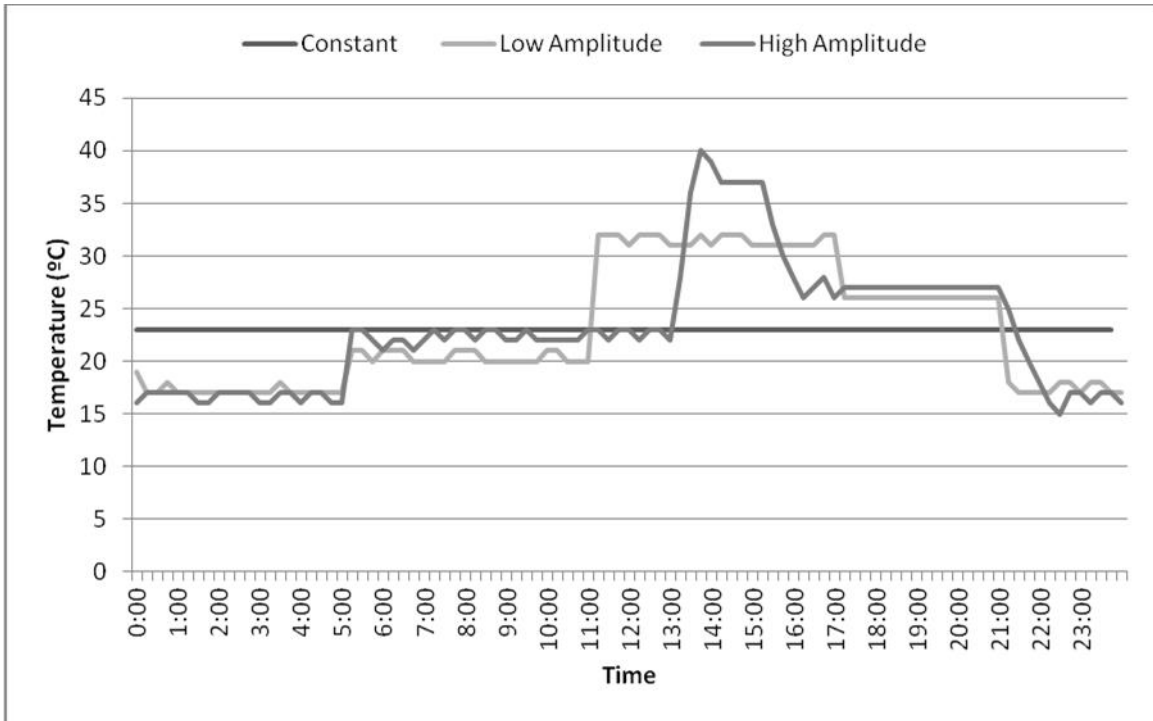


Figure 2.1: Daily temperature (°C) for each temperature regime.

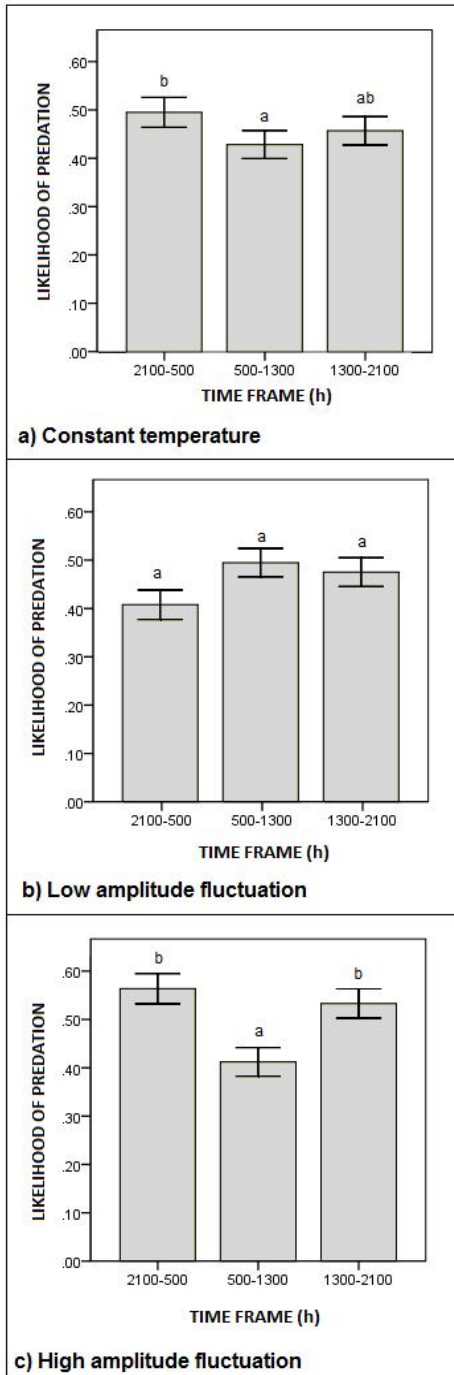


Figure 2.2: Likelihood of *D. hesperus* preying on *E. kuehniella* eggs occurring (mean ± SE) during each of the three time frames in each of the temperature regimes. Within each temperature regime, means followed by the same letter are not statistically significant ($p > 0.05$).

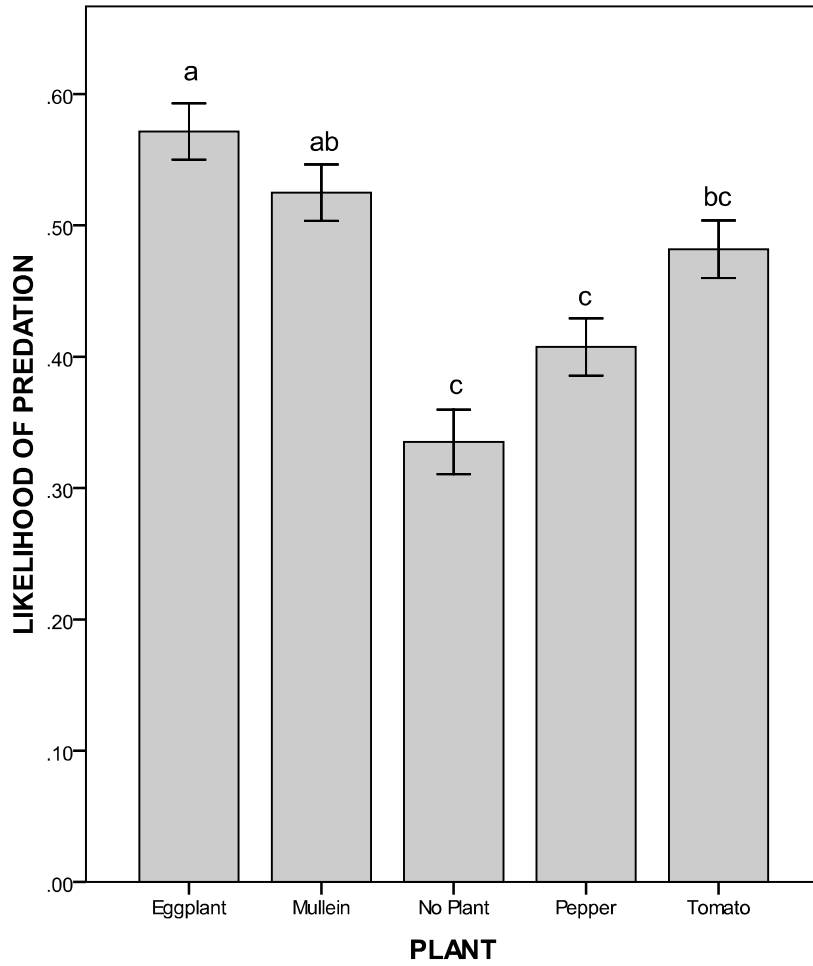


Figure 2.3: Mean (\pm SE) likelihood of *D. hesperus* consuming prey during an eight hour time block on host plants eggplant, mullein, no plant, pepper and tomato (timeframe and temperature regime pooled). Means followed by the same letter are not statistically significant ($p > 0.05$).

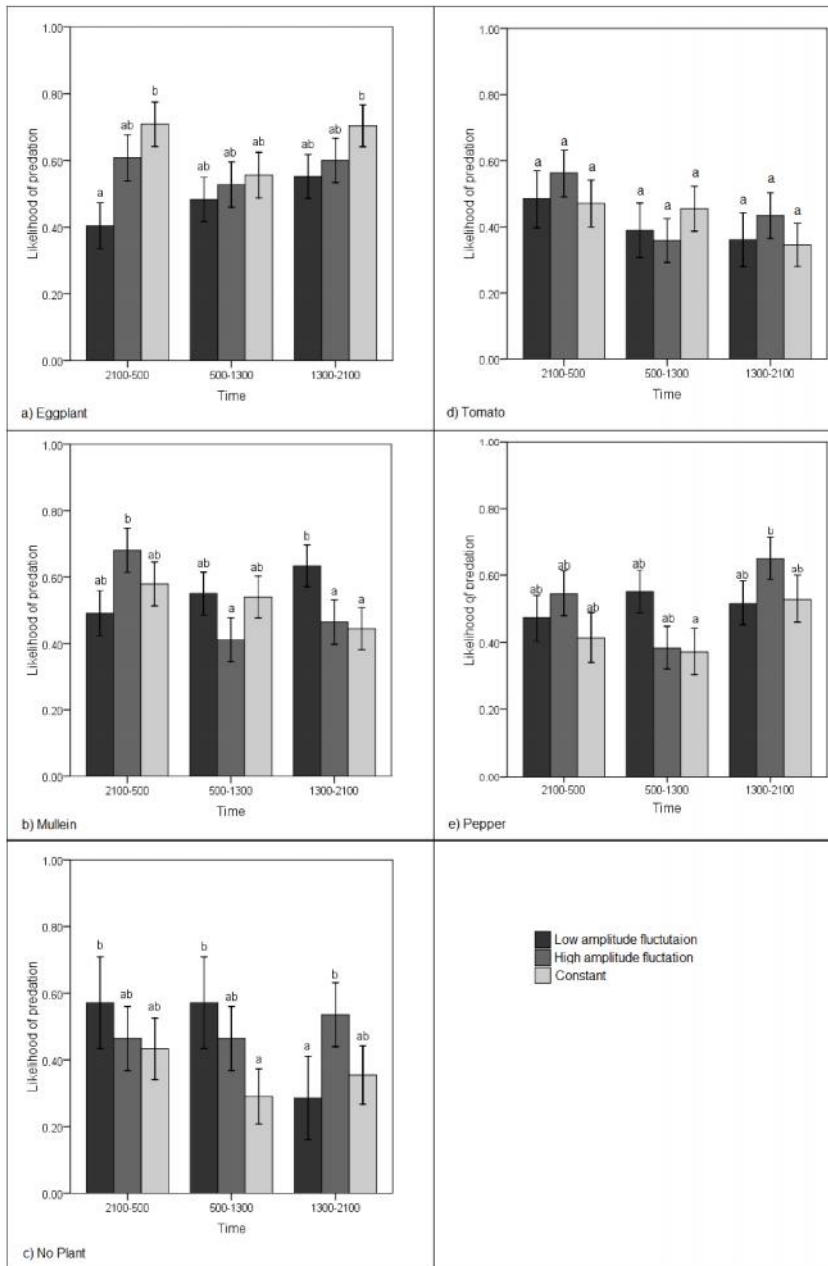


Figure 2.4: Likelihood of *D. hesperus* preying on *E. kuehniella* eggs (mean \pm SE) on host plants: a) eggplant, b) mullein, c) no plant, d) pepper and e) tomato, during each of the three time frames in each of the temperature regimes. Within each host plant, means followed by same letter are not statistically significant.

**CHAPTER 3 : ADAPTIVE FORAGING BEHAVIOUR OF AN OMNIVOROUS
PREDATOR IN RESPONSE TO TEMPERATURE FLUCTUATION**

Introduction

Climate change has implications for many aspects of biology. It is well documented that the mean global temperature is rising and many other effects of global climate change are occurring or are expected to occur in the near future (Meehl and Tebaldi 2004, Solomon 2007). Temperature fluctuation is one of the many expected effects of climate change; it is predicted that temperature extremes will be greater and occur more frequently (Meehl and Tebaldi 2004). All organisms will be affected either directly or indirectly, but insects are particularly vulnerable to these changes as their biology directly corresponds to the ambient temperature (Gullan and Cranston 2005).

Recent research has examined the effect of fluctuating temperature on foraging parasitoids (Bannerman *et al.* 2011), and suggests that although aphid populations are affected by fluctuating temperatures, the effect on aphid parasitoids is minimal. Therefore, demonstrating that the effect of fluctuating temperatures varies across species and has the potential to change trophic level interactions when predator or prey are differentially affected.

A key element to successfully utilising a biological control agent is understanding its foraging behaviour (DeBach and Rosen 1991). Foraging behaviour depends on several factors, including prey abundance, type and quality (Price *et al.* 1980, Eubanks and Denno 2000) and the surrounding environment. Environment is perhaps one of the most important factors driving foraging behaviour of mirid omnivores, in which plant type, leaf structure, temperature, humidity, photoperiod and time of day all have an effect. Sparkes (chapter 2) showed that *Dicyphus hesperus* Knight (Heteroptera: Miridae) was more likely to feed on prey, during a defined period, while on eggplant or mullein plants

than while on pepper or tomato plants, and that the probability of feeding varied with temperature and time of day. Perdikis *et al.* (1999, 2004) found that *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) consumed more aphids while on pepper plants than eggplant but that this varied considerably with temperature and photoperiod. *Orius tristicolor* White (Hemiptera: Miridae) consumed more mites at 33°C than at 25.5°C (Askari and Stern 1972) and *M. pygmaeus* consumed more aphids at 30°C than at 20°C or 25°C (Perdikis *et al.* 1999). VanLaerhoven *et al.* (2003) saw an increase in activity, ability to locate prey and predation rate of *D. hesperus* during the overnight period and Perdikis *et al.* (2004) recorded an increase in number of prey consumed by *M. pygmaeus* during the night.

In chapter two, I examined the effect of fluctuating temperature on total prey consumption and the likelihood of prey consumption of *D. hesperus* in three defined time frames (500-1300h, 1300-2100h and 2100-500h). Results from this work indicated that although the total number of prey consumed by *D. hesperus* in 24 hours was the same in a constant temperature, low amplitude and high amplitude temperature fluctuation, the time at which the predation was occurring differed among temperature regimes. Further observations by Sparkes (personal observations) indicated that during periods of extreme heat, *D. hesperus* did not perform any activity. Together, these results and observations suggest that in order to make up the difference in prey consumption during the periods of extreme heat, *D. hesperus* will have to increase prey consumption at another point during the day.

The following presents results of a study looking at the effect temperature fluctuations; low and high amplitude compared to a constant temperature. The experiment uses the same temperature regimes as presented in chapter two (Sparkes;

unpublished data). The study differs from most other studies examining the effects of fluctuating temperature in that all three regimes used here maintain the same 24 hour mean temperature. The foraging behaviour of individual *D. hesperus* was tracked throughout a 24 hour period (one cycle of the temperature fluctuation) to gain a better understanding of the behavioural changes (with specific emphasis on the feeding behaviour) that occur as a result of the temperature fluctuation.

Materials and Methods

Insect rearing

Omnivore

Laboratory colonies were established using *D. hesperus* that was originally captured from white stem hedge nettle (*Stachys alben* A. Gray (Lamiaceae)) near Woody, California USA (35°42'15"N, 118°50'00"W) at an elevation of ca. 500 m. These colonies were maintained at 25 ± 1°C, 50% RH and 16:8 L:D photoperiod. *D. hesperus* were reared on tobacco *Nicotiana tabacum* L. (Solanaceae) and fed previously frozen *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs *ad libitum*. Eggs were obtained from Beneficial Insectary Inc., Guelph, ON, Canada.

Prey

Trialeurodes vaporariorum Westwood (Homoptera: Aleurodidae) originally collected from commercial greenhouses in Leamington, ON, Canada were maintained in greenhouse colony at the Greenhouse and Processing Crops Research Center in Harrow, ON, Canada on tomato plants. Clean tomato plants were placed into the colony for 24

hours to allow for whitefly oviposition. Eggs were then allowed to develop to the pupal stage prior to use.

Temperature Regimes

To simulate climate change projections, Conviron environmental cabinets were set to one of three climate regimes; constant 23°C, low amplitude fluctuation (17-32°C) and high amplitude fluctuation (17-39°C) (Figure 3.1). All three climate regimes maintained a 24 hour mean temperature of 23°C, and a photoperiod of 16:8 (L:D) both of which are within the optimum range for the study species (Gillespie and Sanchez 2004). The dark period was from 2100 to 0500 hours. In addition, vapour pressure deficit (VPD) was maintained within the optimum range for greenhouse vegetable production (Ontario Ministry of Food and Agriculture 2009) by fluctuating relative humidity within the cabinets. VPD ranged from 0.7-2.17 kPa and thus, relative humidity ranged from 69-90%.

Predation activity data collection

One week post-eclosion, female *D. hesperus* were removed from colony and starved of prey, but provided leaf tissue for 72 hours. Forty-eight hours into the starvation period, the *D. hesperus* were transferred into individual plastic Petri dishes (90 x 15 mm). Each Petri dish had three holes in the bottom, measuring 10 mm in diameter, all covered by a fine mesh, to allow ventilation. Dishes were placed into one of three growth chambers, each set to one of the temperature regimes, for the final 24 hours of starvation. A single tomato leaflet, covered in whitefly scales (minimum 40 scales), was added to each Petri dish. Nine observations were made over the next 24 hours (timing listed in Table 3.1).

The instantaneous behaviour of each *D. hesperus* was recorded. Possible observations included: prey feeding, plant feeding, walking/searching, hiding under the leaf, agitated and no action (Table 3.2). Twenty-nine *Dicyphus* were observed for each treatment.

Results

Different patterns of behaviour were evident between the three temperature regimes (Figure 3.2, Figure 3.3, Figure 3.4). No statistical analyses were carried out on this dataset however several trends were observed. At the constant temperature, *D. hesperus* engaged in all seven of the possible activities. Prey feeding occurred at all observation times, although more individuals were observed prey feeding in the evening than during the morning and early afternoon periods. Plant feeding and walking/searching also occurred at all observation timings, however, plant feeding was lowest at 1400 hours and 2300 hours. At 1400 hours, there was a peak in the number of *D. hesperus* individuals performing no action.

In the low amplitude fluctuation treatment, all seven actions were also observed. Prey feeding was recorded most frequently at the 1700 and 2000 hour observations. Plant feeding was never observed in more than 20% of the individuals at a single observation period in this treatment. The lowest number of *D. hesperus* were observed plant feeding at the 1700 hour observation. At the time of the sharp temperature increase (1100 hours), there was a peak in the number of agitated individuals and a decrease in the number of individuals performing no action.

The activity pattern of *D. hesperus* was quite different in the high amplitude fluctuation than in the other two temperature regimes. Prey feeding was not observed at the 1400 hour observation timing and there was a much greater range in the proportion of

D. hesperus prey feeding across the observation timings. Over 60% of individuals were prey feeding at 2300 hours. This is a greater percentage than any other timing in all treatments. Plant feeding in this treatment was low during the hot periods (1300 hours – 2000 hours). In general, less walking/searching behaviour was observed in the high amplitude fluctuation treatment than the other two temperature regimes and more hiding. Like in the low amplitude fluctuation but to a greater extent, at the time when the temperature rapidly increased (1300 hours in this case), several individuals became agitated, many attempting to fly out of the Petri dish. However, unlike the low amplitude fluctuation, this was followed by only either no action or hiding at the next observation.

Discussion

This study demonstrates that the amplitude of temperature fluctuations has an effect on the predation behaviour of the omnivorous mirid, *D. hesperus* but, that observed behaviours of individuals in the constant temperature are similar to that observed in the low amplitude fluctuation. The most notable differences observed in the high amplitude fluctuation occur as a result of the extreme high temperature. The maximum temperature for this study was specifically chosen to be outside of the optimal temperature range for this species (in development studies, Gillespie *et al.* (2004) recorded 64% nymphal mortality at 35°C). The *D. hesperus* at this temperature were agitated; as the temperature began to rise, several of the insects tried to fly out of the Petri dishes and once at the maximum temperature, the only activities recorded were no action or hiding. Further observations have shown that subjecting *D. hesperus* to the extreme high temperature (39°C) without time to acclimate results in 100% mortality within five minutes of exposure (personal observation). Insects in this experiment were given 24 hours to

acclimate in the environmental chamber before any observations were recorded. Although there was a high number of individuals agitated as the temperature rose in the high amplitude fluctuation (and to a lesser extent in the low amplitude fluctuation), there was no mortality over the experimental period. The results indicate that the *D. hesperus* is able to adapt to the shift in temperature and expand its temperature range. Similarly, Saleh and Sengonca (2003) found that *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) was able to survive, develop and feed on prey in extreme high temperatures only in the fluctuating temperature regimes. This ability to extend the temperature range has also been noted in other insects such as green peach aphids (Davis *et al.* 2006, Hazell *et al.* 2010).

Previous research has shown that plant feeding (or access to water) in *D. hesperus* is necessary for prey feeding to occur and that plant tissue is a source for supplementary nutrients (Gillespie and McGregor 2000). Water is required for extra-oral digestion, the process of prey feeding used by *D. hesperus* (Sinia *et al.* 2004) and plant feeding is a means of acquiring the necessary water.

Further water loss at high temperatures is also of concern and one hypothesis was that *D. hesperus* would increase plant feeding at the higher temperatures to combat this additional water loss. Results here show that following short periods of extreme heat there is no increase in plant feeding. This is not to say that water loss is not a concern at high temperatures. *Dicyphus hesperus* does appear to spend more time resting and hiding during the periods of high heat, a behaviour that may be linked to water conservation. Additionally, the prey source used in this experiment (whitefly) are water rich and may be acting as the water replenishment source.

Previous studies have shown that some species of omnivorous mirids are more active and consume more prey overnight than during the day (Perdikis *et al.* 1999, VanLaerhoven *et al.* 2003, Perdikis *et al.* 2004). Predation rate of *D. hesperus* was examined under various diel patterns at a constant temperature (VanLaerhoven *et al.* 2003) and the predation rate of *M. pygmaeus* was examined under various diel patterns, temperatures and host plants (Perdikis *et al.* 1999, 2004). All of these studies have demonstrated higher activity levels and greater prey consumption overnight than during the day and specifically with regards to temperature, Perdikis *et al.* (1999, 2004) have shown that this relationship is greatest at higher temperatures. Results presented here indicate that during the overnight (dark) periods, greater numbers of *D. hesperus* were observed prey feeding in all treatments, but this trend is greatest in the high amplitude fluctuation. Both temperature and diel pattern are likely to play a part in this behaviour.

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Tables

Table 3.1: Time of each recorded observation and the corresponding temperatures of each treatment during the observation.

Time of observation (h)	Temperature (°C) at each observation		
	Constant	Low Amplitude Fluctuation	High Amplitude Fluctuation
0500	23	17	16
0800	23	21	23
1100	23	32	22
1230	23	32	23
1300	23	31	28
1400	23	32	39
1700	23	32	28
2000	23	26	27
2300	23	18	17

Table 3.2: Description of recorded activities of *D. hesperus* on tomato leaflets with whitefly scales.

Activity number	Activity name	Description
0	No action	The individual is standing still, its proboscis is not moving and is not inserted into the leaf or prey.
1	Hiding	The individual has retreated to the underside of the leaf – any activity here is not visible to the observer.
2	Ovipositing	The individual is ovipositing into the leaf tissue, it is in an upright position and the ovipositor is inserted into the leaf.
3	Walking/searching	The individual is moving around the dish at a normal pace or is stationary but searching for food with its antennae.
4	Plant feeding	The individual is plant feeding, the proboscis is inserted into the leaf tissue.
5	Prey feeding	The individual is prey feeding, the proboscis is inserted into a whitefly scale.
6	Agitated	The individual is moving very fast around the dish or attempting to fly away. The behaviour is very erratic.

Figures

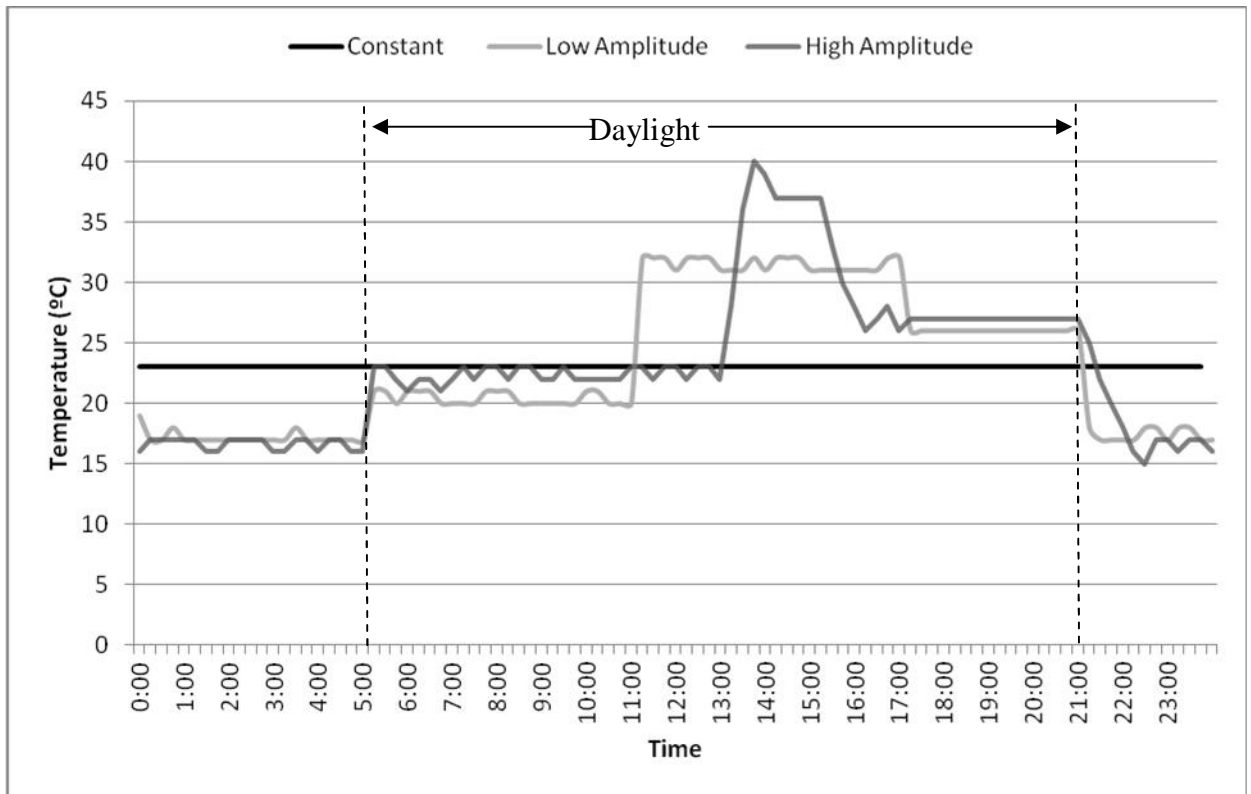


Figure 3.1: Daily temperature (°C) for each temperature regime.

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Figure 3.2: Frequency of *D. hesperus* performing each action at each observation period in the constant temperature regime (n=29).

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Figure 3.3: Frequency of *D. hesperus* performing each action at each observation period in the low amplitude fluctuation temperature regime (n=29).

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Figure 3.4: Frequency of *D. hesperus* performing each action at each observation period in the high amplitude fluctuation temperature regime (n=29).

**CHAPTER 4 : ADULT LONGEVITY OF *DICYPHUS HESPERUS* KNIGHT
(HETEROPTERA: MIRIDAE) UNDER FLUCTUATING TEMPERATURES**

Introduction

As poikilothermic organisms, insects are strongly influenced by temperature. Temperature affects an insects movement, predation, oviposition and development (Gilbert and Raworth 1996). Each insect's development varies along a temperature curve. As temperature increases, towards an upper threshold, development rate increases. Egg development and emergence time decrease, nymphal development time decreases and therefore the time required for stage progression decreases; and adult longevity is reduced (Gullan and Cranston 2005). Once the temperature reaches an upper threshold, development is halted, reproduction may fail and if exposure lasts long enough then the insect will eventually die (Andrewartha and Birch 1954, Danks 1987).

Temperature constantly fluctuates in a diurnal pattern. This pattern is expected to change with global climate change to include an increase in the frequency and severity of temperature fluctuations (Meehl and Tebaldi 2004, Solomon 2007). Due to their large volume to surface ratio, insects physically, respond very quickly to changes in temperature (May 1985) and are expected to be greatly influenced by severe fluctuations. The literature on the effects of diurnal temperatures on insects is contradictory (Eubank *et al.* 1973). Studies have shown that diurnal temperature fluctuations can have a positive effect; a negative effect; or no effect on insect development (see references within Behrens *et al.* 1983). Although there is ample research on the effects on fluctuating temperature on insect populations, the literature exploring the effects of temperature fluctuations above the upper threshold is limited. Gillespie *et al.* (2011) examined the effect of simulated heat waves on a tritrophic food web of pepper plants, aphids and two aphid parasitoids. Gillespie *et al.* (2011) found that aphid population growth was slowed

in high frequency temperature fluctuations compared low frequency temperature fluctuations; however, the specific reason for this is still unclear. Parasitoid development time was also slowed in the high frequency temperature fluctuations.

Predatory Heteroptera are considered an important component of the arthropod fauna in both natural and managed environments (Coll and Ruberson 1998, Saleh and Sengonca 2003). Numerous species of predatory Heteroptera are available commercially and widely used for augmentative biological control of various insect pests (Coll and Ruberson 1998). To successfully utilize a biological control agent, it is important to have a good understanding of how that species will respond to changes in the environmental conditions (Fisher *et al.* 1999). *Dicyphus hesperus* Knight (Heteroptera: Miridae) has been the subject of much research throughout the last decade and shows promise as a biological control agent of various insect pests in greenhouse vegetable production (McGregor *et al.* 1999). *Dicyphus hesperus* is widely distributed throughout North America (Kelton 1980, Henry and Wheeler 1988). This species readily consumes a variety of insect species (Gillespie and McGregor 2000, McGregor and Gillespie 2005, Shipp and Wang 2006) and is considered an obligate omnivore, as it requires plant consumption as well (Gillespie and McGregor 2000). This species was proposed as a biological control agent in greenhouse vegetable crops as it has the potential to control several different pest species as well as the ability to establish and persist in the absence of any pests.

Temperature specific research with respect to *D. hesperus* has been limited to constant temperatures. Gillespie *et al.* (2004) found that two populations of *D. hesperus* from different geographical locations in North America did not differ in their cumulative temperature requirements however, mortality rates of the California population at high

temperatures (35°C) was more than twice that of the British Columbia population. Research has demonstrated that *D. hesperus* have preferences for certain host plants and that development time, fecundity and longevity were also affected in various ways (Sanchez *et al.* 2004). I showed (Chapter 2) that host plant can also have an effect on the predation by *D. hesperus* and that there was a significant effect of the interaction between host plant, temperature regime and time of day but, an understanding of this interaction remains unclear.

The present research aims to compare adult longevity of *D. hesperus* at three temperature regimes (two temperature fluctuations and a constant temperature) and on five host plants. The fluctuations are based on 1) a natural diurnal temperature curve and 2) an example of an extreme temperature event that we may expect from continued climate change. The key to this study is that all three temperature regimes have the same daily mean temperature of 23°C and thus, all subjects would have had an equal number of accumulated degree hours. The hypothesis was that adult longevity would be affected by temperature regime, with shortest longevity being observed in the high amplitude fluctuation. It was also hypothesized that this interaction would be affected by host plant species, with preferred plants such as eggplant and mullein increasing the longevity of *D. hesperus* in all treatments, but to a greater degree in the high amplitude fluctuation where the insects are exposed to a stressful environment and require more from the host plant (e.g. nutrients and protection).

Materials and Methods

Insect rearing and origins

Dicyphus hesperus, originally captured near Woody, California USA (35°42'15"N, 118°50'00"W) were used in this experiment. Colonies were established and maintained at $25 \pm 1^\circ\text{C}$, 50% RH and 16:8 L:D photoperiod on tobacco *Nicotiana tabacum* L. (Solanaceae) and a diet of previously frozen *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs (sourced from Beneficial Insectary Inc., Guelph, ON, Canada) *ad libitum*.

Temperature Regimes

Three temperature regimes were used to simulate climate change projections: constant 23°C, low amplitude fluctuation (ranging from 17-32°C) and high amplitude fluctuation (ranging from 17-39°C) (Figure 4.1). All three temperature regimes maintained a 24 hour mean temperature of 23°C, consistent with the optimal temperature of *D. hesperus* (Gillespie and Sanchez 2004) and the same photoperiod of 16:8 (L:D). Relative humidities fluctuated along with the temperature. Values were chosen to keep vapour pressure deficit (VPD) within the recommended range for greenhouse production of tomato crops (Ontario Ministry of Agriculture and Food 2010). VPD was maintained between 0.70 – 2.17 kPa and thus relative humidity ranged from 69-90%.

Experimental protocol

Four plant species as well as a no plant treatment were used in this trial. Plants used were; Tomato (*Lycopersicon esculentum* Mill. cv. Rhapsody (Solanaceae)), pepper (*Capsicum annuum* L. cv. Bellboy (Solanaceae)), eggplant (*Solanum melongena* L. cv. Black Beauty (Solanaceae)), and mullein (*Verbascum thapsus* L. (Scrophulariaceae)). Leaf disks (2 cm²) of each plant type were set in a prepared Agar gel in a Petri dish (90mm diameter). Each Petri dish had three holes in the top, measuring 10 mm in

diameter, all covered by a fine mesh, to allow ventilation. A single one-week post-eclosion mated female *D. hesperus* was removed from colony and added to each dish. Petri dishes were then placed into one of three growth chambers, each set to a different temperature regime. *Ephestia kuehniella* eggs were added to each dish daily (numbers well in excess of what could be consumed in one day). Adult longevity (days) were recorded at the time of death of each insect.

Data Analysis

Adult longevity data were analysed using Cox proportional hazards model.. Proportion of *D. hesperus* surviving in each of the three temperature regimes was plotted over time.

Results

Dicyphus hesperus lived longer in the constant temperature regime (median=20, 95% CI; 16, 24 days) [n=56]) than in either of the two fluctuating temperatures (low amplitude: median=13, 95% CI; 7.54, 16 days [n=55]; high amplitude: median=10, 95% CI; 8, 12 days[n=56]; ($p < 0.001$). *Dicyphus hesperus* longevity when in the no plant treatment was greatly reduced (median=4.9, 95% CI; 3.2, 11) compared to eggplant (median=16, 95% CI; 11, 20), mullein (median=16, 95% CI; 13, 20), pepper (median=13, 95% CI; 8, 19) and tomato (median=11, 95% CI; 8, 17) treatments. A restricted analysis with no plant data excluded showed that plant type did not affect adult longevity ($p=0.367$) nor did the interaction between plant type and temperature regime ($p=0.273$)

Survivorship curves were plotted for each plant in each temperature regime (Figure 4.2). Survivorship in the three temperature regimes was quite varied; in the first day there was approximately ten percent mortality in the high amplitude fluctuation,

compared to no mortality in the other two treatments. In the first five days mortality was similar across the three treatments. Between the seventh and tenth days the mortality in the constant temperature regime decreased while in the high amplitude fluctuation it was quite high, and the low amplitude fluctuation intermediate. By day 25 there were no survivors in the high amplitude fluctuation, fewer than 10% in the low amplitude fluctuation and approximately 30% in the constant temperature regime (Figure 4.2).

The main difference in the survivorship curves between plants was the no plant treatment. In all three temperature regimes there was a much higher rate of early mortality in the no plant treatment compared to the four plant species. In all three temperature regimes more than 50% of *D. hesperus* were dead before ten days had past. Interestingly, in the high amplitude fluctuation this was also true of the pepper treatment.

Discussion

Although all temperature regimes had the same daily mean temperature, the adult longevity was different between treatments. Adult female *D. hesperus* lived, on average, 19.0 days in the 23°C constant temperature, 13.9 days in the low amplitude fluctuation and 11.1 days in the high amplitude fluctuation. These results are consistent with the notion that fluctuating temperatures will affect physiological time, which is the amount of heat required over time for an insect to complete development (Gullan and Cranston 2005). Gillespie *et al.* (2004) found that temperatures of 35°C caused a nymphal mortality of 64% in this particular population (collected from California) so one may expect that some of the reason for the reduced mean adult longevity in the high amplitude fluctuation may be a result of increased mortality caused by the extreme temperatures (or the rate at which they increase) rather than the insects completing their lifecycle naturally.

This effect is difficult to quantify; however, I suspect that it is fairly low as the survivorship curve shows a similar initial mortality among all temperature regimes.

As expected, plant species also affected the adult longevity. *Dicyphus hesperus* adults lived the longest when on mullein and eggplant, followed by tomato and pepper and the shortest without any plant. Sanchez *et al.* (2004) found that *D. hesperus* had strong preferences for some plants over others. Their study also showed that some plants provided more nutritional quality than others. Mullein was the only plant species tested by Sanchez *et al.* that provided enough nutrients to the insects that they did not require any prey to reproduce. In Chapter two, I included eggplant in studies with *D. hesperus* and found that prey consumption was significantly higher while on mullein and eggplant than the other plant species tested. Specific reasons why mullein and eggplant produce different results than other plants are unclear. One possible explanation is the microclimate created by the leaf surface. Both mullein and eggplant leaves are quite hairy compared to the leaves of pepper and tomato plants. The hairs on the leaves may affect the microclimate that the *D. hesperus* is exposed to by increasing the boundary layer associated with the leaf and may protect the insect during periods of rapid temperature increase. There will also be differences in leaf microclimate caused by different levels of transpiration on each plant type. A high level of transpiration will cool the leaf surface and therefore reduce the extremity of temperatures.

There was no statistical significance of the interaction between temperature regime and host plant species. However, this is an area which requires more exploration. It is clear that both factors are important when considering adult longevity (an important point when utilizing as a biological control agent) and a better understanding of these factors could explain why specific host plants are considered to be higher quality. Further

research should be conducted to address what attributes the high quality host plants have which make them more suitable for the insects. This may include any number of factors including physical structure or nutrients.

This study emphasizes that fluctuations in temperature can greatly affect the adult longevity of *D. hesperus*. Further studies looking at nymphal development and mortality as well as reproductive period and offspring numbers under fluctuating temperatures would be useful to the utilization of *D. hesperus* as a biological control agent as well as to the greater context of the effects of increased amplitude temperature fluctuation on this and similar species.

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Tables

Table 4.1: Mean longevity (days) +/- SE of *D. hesperus* on each of the five plant types. Means followed by the same letter are not statistically significant ($p>0.05$).

Plant Type (n)	Mean Longevity (days) +/- SE
Eggplant (33)	16.5 +/- 1.57 ^a
Mullein (34)	18.4 +/- 1.57 ^a
No Plant (33)	9.53 +/- 1.69 ^b
Pepper (33)	14.1 +/- 1.50 ^{ab}
Tomato (34)	14.6 +/- 0.73 ^{ab}

Figures

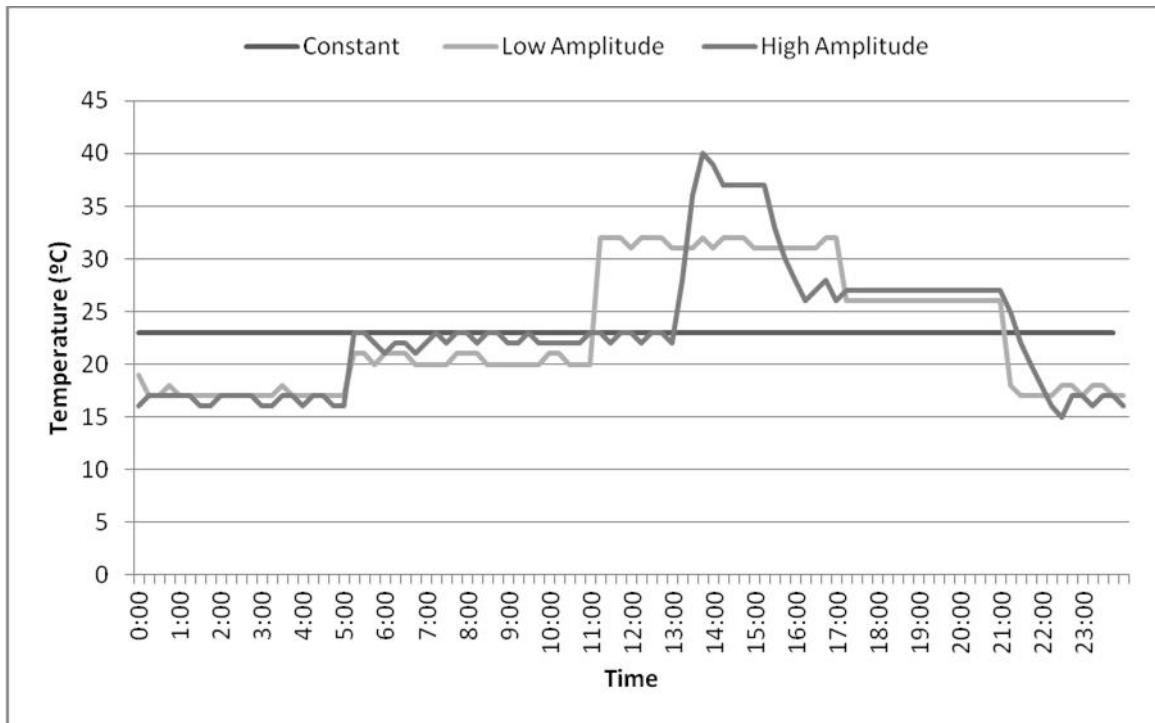


Figure 4.1: Daily temperature (°C) for each temperature regime.

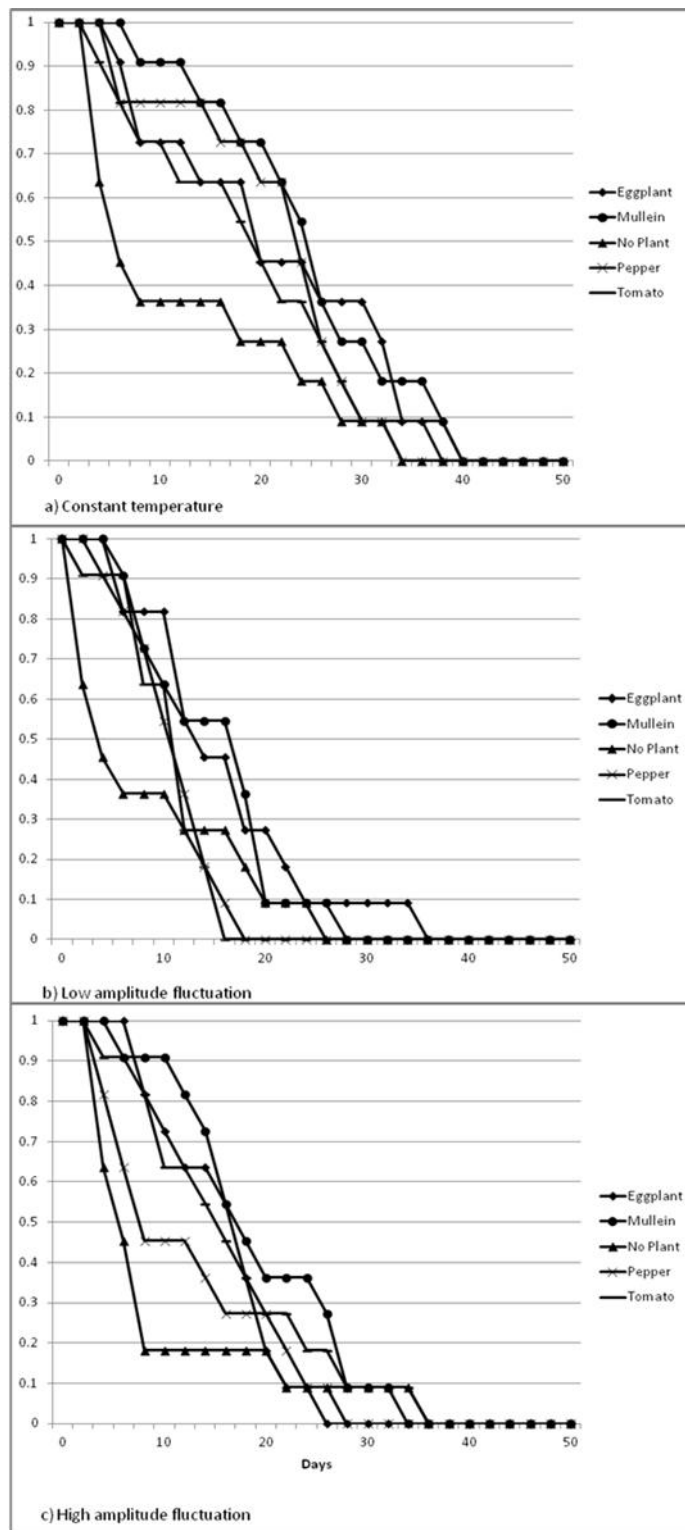


Figure 4.2: Proportion of *D. hesperus* surviving over time on each plant type in the a) constant temperature, b) low amplitude fluctuation and c) high amplitude fluctuation.

CHAPTER 5 : DISCUSSION

This work examined the effect of low and high amplitude temperature fluctuation on predation and longevity of *Dicyphus hesperus* Knight (Heteroptera: Miridae). Along with the mean global temperature rising as a result of climate change, the occurrence of extreme weather events, including higher amplitude temperature fluctuations, are also expected to increase. Currently, most of the climate change literature focuses on the impacts of the rising mean temperature rather than the impact of fluctuating temperature. Here, the specific effect of temperature fluctuation was assessed using three temperature regimes (constant temperature, a low amplitude fluctuation and a high amplitude fluctuation) which all maintained the same twenty-four hour mean temperature and therefore, the same accumulated degree hours.

Total prey consumption and the likelihood that a predation event would occur during defined periods of the day were assessed on four plant species and a no plant treatment. Results from this experiment showed that, when plant type and time frame were pooled, temperature regime had no effect on total prey consumption or likelihood of predation occurring. However, the interaction between temperature regime and time of day did have an effect but there were no consistent trends across treatments. Predation behaviour was then examined to further assess what specific effects the temperature fluctuations were having on individual *D. hesperus*. Observations from this experiment show that temperature fluctuations appear to impact the behaviour patterns of *D. hesperus*. The activity pattern in the high amplitude fluctuation specifically, was quite different from the other two temperature regimes, as there was no prey feeding during the hottest period of the day. In both, the high and low amplitude fluctuations, at the time when the temperature rapidly increased several individuals were agitated and appeared to be trying to escape from the Petri dish.

Lastly, adult longevity was measured on the five host plants when exposed to each temperature regime. Adult longevity was negatively affected by fluctuating temperatures and this relationship increased in magnitude with the increase in fluctuation amplitude. Longevity seemed to be affected by host plant; although there was no significant difference among plant species. Eggplant and mullein had the greatest longevity, followed by tomato and pepper and then no plant.

Timing of predation

Previous studies have shown that Miridae species, including *D. hesperus* (VanLaerhoven *et al.* 2003) and *Macrolophus pygmaeus* Rambur (Perdikis *et al.* 1999, 2004) can consume more prey at night than during the day. My results indicate that the likelihood of *D. hesperus* consuming prey is greatest overnight in both the constant and the high amplitude fluctuation temperature regimes but not in the low amplitude fluctuation. Furthermore, closer examination of the predation behaviour during the overnight period reveals that the bulk of prey feeding occurred shortly after nightfall rather than well into the overnight period (Chapter 3). These results indicate that: 1) *D. hesperus* does not necessarily prey more in the evening, but rather if temperature fluctuations increase or decrease in amplitude (simulated in the high amplitude fluctuation and the constant temperature regime) the feeding pattern shifts and 2) when high overnight feeding does occur, it is more likely to occur shortly after nightfall rather than well into the night. This may have implications on food web dynamics, particularly if prey response differs, and an exploration of this would be beneficial. Bannerman *et al.* (2011) demonstrate that the effect of temperature fluctuation can have different impacts on different trophic levels.

Host plant

The inclusion of various plant species (tomato, pepper, eggplant, mullein and no plant) was an important component of this work. *Dicyphus hesperus* performs differently on different plant types (Sanchez *et al.* 2004). Mullein is a preferred host plant for this species and the only known plant type that is able to support *D. hesperus* throughout its entire life cycle and allow for reproduction. Tomato and pepper plants are two of the most commonly grown greenhouse vegetables in Canada; both are crops which would be suitable for the deployment of biological control agents (i.e. *D. hesperus*) yet both are considered to be of considerably lower quality. In the presence of prey, *D. hesperus* was able to complete development on all plant species tested (Sanchez *et al.* 2004). Eggplant was not included in the Sanchez *et al.* experiment (2004) but is also a crop grown under protection in Canada. Eggplant is physically quite similar to mullein particularly with respect to the thick hairs covering the leaf surface. Eggplant has also been shown to be a higher quality plant than pepper to the closely related species, *M. pygmaeus* (Perdikis *et al.* 1999). Similar to differences in host plant preference from Sanchez *et al.* (2004), predation likelihood varied across host plant. The greatest likelihood of predation occurred on eggplant and mullein followed by tomato, pepper and no plant. Nymphal development time of *D. hesperus* also varies across host plants, with development time and nymphal mortality lowest on mullein (Sanchez *et al.* 2004). Here, adult longevity was examined but the only statistically significant difference was between the no plant treatment (lowest adult longevity) and eggplant or mullein (greatest adult longevity) (Chapter four).

Leaf microclimate likely played an important role in these experiments. Generally speaking, leaf microclimate will be different than the ambient conditions and the

microclimate will affect the predator. Specifically, leaf temperature has been shown to influence the predation and oviposition by *Neoseiulus cucumeris* (Acari: Phytoseiidae) (another biological control agent used in greenhouse vegetable crops) (Jones *et al.* 2005). In the work presented here, microclimate was not assessed nor was the difference in microclimate between plant species. The leaf microclimate of each plant type will differ due to differences in physical structure, transpiration and vapour condensation and therefore it is likely that extremity of temperatures and the rate at which they change differ between plant treatments. Depending on the level of difference between plant types this may have an effect on results. Further work on the microclimate of each plant type during the temperature fluctuations would indicate the how much effect this will have had on the results.

Interaction of temperature fluctuation and host plant and time period

One component of this work that remains largely unanswered is the interaction of the three treatment factors: temperature fluctuation, host plant and time period. Results from experiment one showed that the interaction of these factors did have a significant effect on the likelihood of predation. The interaction however, was difficult to interpret as there were no clear trends in these differences.

Dicyphus hesperus as a model system

This study focused on a specific predator, *D. hesperus*, but the results may be applicable to the effects of climate change on other mirid species or more generally speaking, other omnivorous arthropods. Several closely related species are used as biological control agents in glasshouse vegetable crops. Results may have applications

with other *Dicyphus* spp., *Nesidiocoris* spp., *Macrolophus* spp., and *Orius* spp., for example.

The research focus on an increasing mean temperature is valid yet we should also consider more closely the implications of other impacts of climate change. Here, an increased amplitude fluctuating temperature, as is predicted to occur has resulted in changes to predation behaviour as well as adult longevity. Consideration of the effects of fluctuating temperatures should be included in future arthropod studies.

***Dicyphus hesperus* as a biological control agent**

Dicyphus hesperus has practical applications as a biological control agent in North American greenhouse vegetable crops; however as of yet its potential has not been realized. One of the limitations to its use has been the need to establish a population of the predator in periods before to a pest outbreak and then sustain the population afterwards. It has been suggested that mullein be used to aid in population establishment (Sanchez *et al.* 2003) and results shown here are consistent with that notion. While on host plant mullein, *D. hesperus* are more likely to consume prey and have a longer adult longevity (and thus predation capability) than when on crop plants tomato and pepper. Eggplant has also been included as a host plant in the study. *Dicyphus hesperus* performed similarly on eggplant and mullein both in likelihood to prey feed and adult longevity. This indicates a potential to use eggplant as an establishment plant in other greenhouse crops and also great potential to use *D. hesperus* as a biological control agent in eggplant. Eggplant is a minor crop and greenhouse production can be difficult as many pests are attracted to the crop (Lee *et al.* 2009). Yet *Dicyphus hesperus* has been successfully applied for biological control of pests on eggplant in The Netherlands and

British Columbia, Canada (D. Gillespie Per comm. 2012) and other mirid species have been successfully utilized as biological control agents in eggplant crops in Europe (Perdikis *et al.* 2008) and Japan (Nakaishi and Arakawa 2011).

There is also potential to use *D. hesperus* as a biological control agent on eggplant currently used as a trap plant in other greenhouse crops, such as poinsettia or tomatoes, to instead use the eggplant as both a trap and a banker plant for the *D. hesperus*. In this scenario the predator could be pre-established on the eggplant prior to its addition to the greenhouse (Huang *et al.* 2012). As pest numbers rose they should be attracted to the eggplant which would already have the population of *D. hesperus* established.

Conclusions

This work demonstrates the possible consequences of increased temperature fluctuation on *D. hesperus*. Amplitude of fluctuation has an effect on both predation and adult longevity. Plant species may act to mediate these effects through different leaf microclimate.

The effect of temperature fluctuation on predation and predation behaviour will have implications in both managed (e.g. greenhouse) and natural ecosystems. Not only will the predator experience changes but all trophic levels will be affected. The importance of temperature fluctuation then becomes a question of the interaction of trophic levels while affected by the fluctuations.

The amplitude of temperature fluctuation also affects the longevity of *D. hesperus* which again will have implications beyond this single species. What is not clear is what is causing the change in longevity; increased mortality as a result of stress or a natural

lifespan affected by a change in accumulated temperature. Further work to establish the root cause of the change in longevity would be necessary.

Climate change is occurring. One of many consequences will include greater frequency and amplitude of temperature fluctuations. The overall effect of these changes will not be measured by the effect on one species but rather the summation of effects on all trophic levels within an ecosystem. Understanding the effect on individuals and the relationship between trophic levels will be key to understanding the implications of increased temperature fluctuations in the future.

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