THE IMPACTS OF EXTREME FLUCTUATING SUMMER TEMPERATURES ON APHID-PARASITOID INTERACTIONS AND COMMUNITY DYNAMICS

by

Jordan Allen Bannerman
B.Sc. (Hons.), University of British Columbia Okanagan, 2008

THESIS
SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF PEST MANAGEMENT

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY

Fall 2011

Approval

Name: **Jordan Allen Bannerman**

Degree: **Master of Pest Management**

Title of Thesis: **THE IMPACTS OF EXTREME FLUCTUATING SUMMER TEMPERATURES ON APHID-PARASITOID INTERACTIONS AND COMMUNITY DYNAMICS**

Examining Committee:

Chair: **Dr. Gordon L. Rintoul**
Assistant Professor

_____

Dr. Bernard D. Roitberg
Senior Supervisor
Professor

_____

Dr. David R. Gillespie
Supervisor
Research Scientist, Pacific Agri-Food Research Centre, Agriculture and Agri-Food Canada

_____

Dr. Jenny S. Cory
Supervisor
Associate Professor

_____

Dr. Deborah Henderson
External Examiner
Director, Institute for Sustainable Horticulture
Kwantlen Polytechnic University

Date Defended/Approved: August 30, 2011

Partial Copyright Licence

Abstract

Global climate change models predict an increase in the frequency and severity of extreme temperature events in temperate regions. I explored the effects of severe and fluctuating daily temperatures on aphid-parasitoid interactions, parasitoid life history, and community dynamics using both theoretical and experimental approaches. I first modelled the community level effects of daily maximum temperatures, the frequency of warmer-than-average days, and the autocorrelation of daily temperatures on a theoretical aphid-parasitoid community. Then I experimentally investigated influence of the frequency and amplitude of daily temperatures on trait-mediated indirect interactions between green peach aphids and *A. matricariae*. Finally, I assessed how development under extreme fluctuating temperature regimes influenced the life history characteristics of *A. matricariae*. The results from my studies suggest that increased frequency and severity of extreme warm temperatures can negatively impact populations, population interactions, and community dynamics.

Keywords: Climate change; Trait-mediated interactions; Trophic interactions; Community dynamics; *Aphidius matricariae*; *Myzus persicae*

Acknowledgements

First, I would like to thank Dr. Bernard Roitberg and Dr. David Gillespie, my co-supervisors for their support and guidance throughout the course of my degree. I could always count on getting excellent guidance when I needed it, but also the freedom to explore and develop my ideas on my own as well. I would also like to thank Dr. Robert Lalonde, my honours thesis supervisor, without his guidance and support during my undergraduate degree, I would not have had an opportunity to join the Roitberg lab.

This work would not have been possible without the generous help provided by Peggy Clarke. The knowledge that everything was always under control when I was not able to be at the research station in person was always reassuring. I would also like to thank Dr. Jenny Cory for her comments and feedback on my thesis work and Dr. Deborah Henderson for her role as my public examiner. I know my thesis is better with their input. My first chapter would have been little more than an idea on paper without the generous coding assistance and instruction provided by Brian Ma, Alex Chubaty, and Mick Wu. When looking for inspiration for areas of research that I would like to pursue, my conversations with Lee Henry were always stimulating and productive.

I would like to thank all of the members of the Roitberg lab and those other individuals that attended our lab meetings and always contributed valuable positive feedback on my work and presentations. I would also like to thank all of the students

who assisted me with my experiments: E. Quan, M. Anaka, Z. Monteith, J. Dubman, J. Scheu, C. Hodson, L. Hart, and A. Nasreen.

The research presented here was supported by Simon Fraser University, the National Science and Engineering Research Council (NSERC), and a NSERC Strategic grant held by both Dr. Roitberg and Dr. Gillespie.

Finally, I would like to thank my parents, family and friends for their ever present encouragement and support.

Table of Contents

List of Figures

List of Tables

1: Introduction

Global climate change represents an environmental disturbance that will lead to shifts in ecosystem dynamics and functioning (Vitousek 1994, Cannell and Thornley 1998, Stenseth et al. 2002, Walther et al. 2002). Increased mean temperatures will be accompanied by an increase in the frequency and severity of localized extreme temperature events, particularly in the temperate latitudes (Bale et al. 2002, Karl and Trenbeth 2003, Meehl and Tebaldi 2004). Many temperate areas could therefore see an increase in episodic periods of extremely warm weather during the summer (De Boeck et al. 2010). These periods of warm weather are generally accompanied by more sunshine and larger vapour pressure deficits than typically occur during summer, which may also act as stressors. In addition to temperature shifts, Carbon Dioxide levels are also predicted to increase. Vapour deficits and CO_2 are not examined in this thesis however. The effects of climate change are more complex than a simple response to increased mean temperatures (Easterling et al. 2000, Walther et al. 2002, Hance et al. 2007, Hazell et al. 2010, Robinet and Roques 2010). But, the implications of an increased frequency of severe high temperature events during the summer on ectothermic organisms have not received much attention to date compared to research focused on the effects of increased mean temperatures and low temperature limitations during the cooler seasons (Hance et al. 2007, Hazell et al. 2010).

Insects, like all ectotherms, are intricately linked to ambient temperature and are extensively influenced by changes in temperature (Huey and Kingsolver 1989, Sibly and

Atkinson 1994, Bale et al. 2002, Angilletta and Dunham 2003, Hance et al. 2007). Temperature influences physiology, development, behaviour and life history of arthropods because their body temperature closely tracks ambient temperature (Roux et al. 2010). All organisms have thermal ranges to which their physiological functions are optimized (Angilletta et al. 2002, Chown and Terblanche 2007). How changing temperatures will affect any given species will depend on its thermal responses and tolerances, which makes it extremely difficult to develop rules to describe the effect temperature will ultimately have on communities (Davis et al. 1998, Harrington et al. 2001, Angilletta and Dunham 2003, Gillespie et al. 2011). It is also difficult to draw general conclusions based on the outcomes of environmental disturbance, like an increased frequency of extreme warm temperature events, on a community, because of the complexity of the responses across study systems (Ives 1995, Cannell and Thornley 1998, Davis et al. 1998, Bezemer et al. 1999, Harrington et al. 2001).

The green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), is a worldwide crop pest that is capable of feeding on over forty plant families causing reduced growth and damage to hosts (Blackman and Eastop 1984). The green peach aphid is also a vector for over one hundred plant viruses, which contribute to significant crop losses (Blackman and Eastop 1984). Aphids are particularly sensitive to changes in temperature due to a range of biological features that they exhibit including temperature dependent development, reproduction and dispersal capabilities (Hulle et al. 2010). Since aphids are also economically significant pest insects, they are excellent model organisms to use to explore the effects of climate change from an individual to the ecosystem level.

Aphidius matricariae (Haliday) (Hymenoptera: Braconidae) is a parasitoid wasp of the green peach aphid, *Myzus persicae* in its native Eurasian range (Giri et al. 1982). It is both ecologically and economically important, and is commercially available as a biological control agent for the control of green peach aphids (D.R. Gillespie Pers. comm.). *Aphidius* wasps are koinobiont parasitoids, and by definition, develop within living aphids until pupation, when they kill their aphid host and pupate within the empty 'mummies'; thus, they have limited mobility throughout their immature development (Stary 1970). This relationship with a living aphid forces the immature parasitoids to deal with their hosts' thermal stress in addition to their own thermal stress for a significant portion of their lifespan (Hance et al. 2007).

The warming associated with climate change is predicted to benefit agricultural pest insects due to an increase in the lower temperatures experienced, which can increase overwinter survival and the ability to produce more generations in a year , and which could lead to an increase in the number of pest outbreaks (Bezemer et al. 1998, Cannon 1998, Bale et al. 2002, Hazell et al. 2010, Roux et al. 2010). Shifts in population dynamics that could allow pests to reach outbreak population levels will have severe implications on a global scale (Bale et al. 2002, Fuhrer 2003). Biological control agents such as *A. matricariae* provide ecologically and economically important services by controlling these pest insects, and their effectiveness may be influenced by climate change. Determining how climate change will influence the pest species, the organisms used to control the pests, and the interactions between the pest and its control organism is a large but important task.

My thesis begins with a broad community level focus that explores how communities are influenced by extreme fluctuating temperatures. I then focus on how extreme fluctuating temperatures influence specific interactions and processes within an aphid-parasitoid community. This approach was used to elucidate the underlying mechanisms which play a role in producing the community and population level impacts that I observed.

In Chapter 2, I develop a stage-structured Leslie population projection matrix model to explore the effects of extreme and fluctuating summer temperatures on the community dynamics of and aphid-parasitoid community. I assess the individual and combined effects of increasing the amplitude of daily temperature fluctuations, increasing the frequency of warmer-than-average days, and increasing the autocorrelation of daily temperatures. I also explore the effects of adding differential susceptibility to temperature-dependent mortality based on aphid age class (instar) on the persistence of the aphid and parasitoid populations.

In Chapter 3, I examine how the severity of a temperature regime impacts the strength of trait-mediated interactions transmitted between the parasitoid and its host. First, I determined the typical level of anti-predator response exhibited by the aphids when confronted with actively foraging female *A. matricariae*. I then subjected aphid populations to one of four different temperature regimes, which differed in the amplitude and frequency of daily heat pulses and applied one of three disturbance treatments, no disturbance, simulated trait-mediated disturbance, or actual female parasitoids. The disturbance treatments allowed me to isolate the impact of trait-mediated disturbance on aphid populations under a range of extreme temperature regimes.

In Chapter 4, I explore the impacts that extreme and fluctuating temperatures during development have on the subsequent life history of adult female *A. matricariae*. As keystone species of ecological and economic importance, it is important to determine the effects of extreme and fluctuating temperatures on parasitiods like *A. matricariae*. Extreme fluctuating periods of temperature are predicted to increase in frequency in the future, and this may impact parasitoids' life history and their ability to control pest insect populations.

The effects of climate change communities cannot be fully explained by solely looking at overall community dynamics. It is also problematic to focus too narrowly on single populations ignoring the interactions occurring within and between trophic levels. In my thesis I examine the effects of extreme and fluctuating temperatures at multiple levels of organization to form a more complete picture of the overall impacts of climate change. I examine how extreme fluctuating temperatures impact community dynamics, population interactions, and individual in an ecologically and economically important community.

1.1 Literature cited

Angilletta, J., M.J. and A. E. Dunham. 2003. The temperature-size rule in ectotherms: Simple evolutionary explainations may not be generated. The American Naturalist **162**:332-342.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. Martijn Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. Hefin Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

Bezemer, T. M., T. H. Jones, and K. J. Knight. 1998. Long-term effects of elevated CO_2 and temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. Oecologia **116**:128-135.

Bezemer, T. M., K. J. Knight, J. E. Newington, and T. H. Jones. 1999. How general are aphid responses to elevated CO_2? Annals of the Entomological Society of America **92**:724-730.

Blackman, R. L. and V. F. Eastop. 1984. Aphids on the world's crops, an identification guide. Wiley, New York.

Cannell, M. G. R. and J. H. M. Thornley. 1998. N-poor ecosystems may respond more to elevated [CO_2] than N-rich ones in the long term. A model analysis of grassland. Global Change Biology **4**:431-442.

Cannon, R. J. C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. Global Change Biology **4**:785-796.

Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. Journal of Animal Ecology **67**:600-612.

De Boeck, H. J., F. E. Dreesen, I. A. Janssens, and I. Nijs. 2010. Climatic characteristics of heat waves and their simulation in plant experiments. Global Change Biology **16**:1992-2000.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate Extremes: Observations, Modeling, and Impacts. Science **289**:2068-2074.

Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO_2, ozone, and global climate change. Agriculture, Ecosystems and Environment **97**:1-20.

Giri, M. K., B. C. Pass, K. V. Yeargan, and J. C. Parr. 1982. Behaviour, net reproduction, longevity, and mummy-stage survival of Aphidius matricariae [Hym. Aphididae]. Entomophaga **27**:147-153.

Hance, T., J. van Baaren, P. Vernin, and G. Boivin. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology **52**:107-126.

Harrington, R., R. A. Flemming, and I. P. Woiwod. 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? Agricultural and Forest Entomology **3**:233-240.

Hazell, S. P., B. P. Neve, C. Groutides, A. E. Douglas, T. M. Blackburn, and J. S. Bale. 2010. Hyperthermic aphids: Insights into behaviour and mortality. Journal of Insect Physiology **56**:123-131.

Huey, R. B. and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. TRENDS in Ecology and Evolution **4**:131-135.

Hulle, M., A. Coeur d'Acier, S. Bankhead-Dronnet, and R. Harrington. 2010. Aphids in the face of global changes. Comptes Rendus Biologies **333**:497-503.

Ives, A. R. 1995. Predicting the response of populations to environmental-change. Ecology **76**:926-941.

Karl, T. R. and K. E. Trenbeth. 2003. Modern global climate change. Science **302**:1719-1723.

Meehl, G. A. and C. Tebaldi. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science **305**:994-997.

Robinet, C. and A. Roques. 2010. Direct impacts of recent climate warming on insect populations. Integrative Zoology **5**:132-142.

Roux, O., C. Le Lann, J. J. M. van Alphen, and J. van Baaren. 2010. How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid Aphidius avenae (Hymenoptera: Aphidiidae)? Bulletin of Entomological Research **100**:543-549.

Sibly, R. M. and D. Atkinson. 1994. How rearing temperature affects optimal adult size in ectotherms. Functional Ecology **8**:486-493.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science **297**:1292-1296.

Vitousek, P. M. 1994. Beyond global warming - ecology and global change. Ecology **75**:1861-1876.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

2: The impacts of extreme and fluctuating temperatures on aphid-parasitoid population dynamics: a theoretical exploration

Jordan A. Bannerman, Bernard D. Roitberg

J. Bannerman designed and coded this model with the help from Dr. Roitberg, Dr. Ma, A. Chubaty and Dr. Wu. J. Bannerman wrote the manuscript for the work presented here.

2.1 Abstract

Climate change is predicted to increase the occurrence of extreme temperature events. I constructed a Leslie matrix model with intra-generational dynamics to explore the impact of extreme and fluctuating temperatures on host-parasitoid population dynamics. I varied three temperature parameters to generate a range of temperature regimes that varied in the daily maximum temperature (and amplitude since the range of daily minimum temperatures was held constant), the number of warmer-than-average days and the autocorrelation of those warmer-than-average days. All three temperature parameters influenced community dynamics. Increasing the daily maximum temperatures and/or the frequency of warmer-than-average days reduced community persistence time and increased the probability of extinction of the aphid and parasitoid populations. The effect of increasing autocorrelation was dependent on the daily maximum temperatures and the frequency of warm days. Population fluctuation decreased with increasing autocorrelation under a low frequency of warm days at intermediate temperatures. The time to extinction increased with increasing

autocorrelation and increasing frequency of warm days. I also assessed if adding additional biologically derived information based on age class of the organisms changed our results. Increasing the temperature dependent mortality rates of juvenile aphid age classes relative to the adult mortality rates increased extinction and further decreased time to extinction in populations that already went extinct. These additional temperature phenomena exert significant effects on community and population dynamics in addition to those produced by changes in mean temperatures.

Keywords: Leslie population projection model; host-parasitoid dynamics; community dynamics; intra-generational dynamics; climate change; heat-shock; *Myzus persicae*; *Aphidius.*

2.2 Introduction

Global climate change and climate fluctuations influence ecological interactions and processes which may subsequently impact population dynamics (Ives 1995, Stenseth et al. 2002, Walther et al. 2002). Climate change models predict both an increase in mean temperatures and the variance associated with the mean (Easterling et al. 2000, Meehl and Tebaldi 2004). Most climate change research has focused on the effects of increased mean temperatures and overwintering temperature with little emphasis on increased summer temperatures and temperature variance; all of these phenomena likely impact trophic interactions and population dynamics since the effects of climate change appear to be more complex than linear responses to increased mean temperatures (Easterling et al. 2000, Walther et al. 2002, Hance et al. 2007, Hazell et al. 2010, Robinet and Roques 2010). In the future, more frequent severe temperature events, particularly events with periods of extreme heat during the summer months in temperate regions may occur (Meehl and Tebaldi 2004). The combined effects of an increased mean along with more, unpredictable, frequent warm temperature events on multiple interacting populations are not obvious (Gillespie et al. 2011), but the effects of these temperature phenomena on species interactions and population dynamics can be modelled so that the individual and combined impacts can be assessed.

The effects of fluctuating temperatures on ectotherms are extensive; their development, behaviour and life history all depend on the ambient temperature (Angilletta et al. 2002, Chown and Terblanche 2007, Roux et al. 2010). Physiological functions have optimal thermal ranges, and when temperatures exceed an organism's optimal range, a range of negative effects may be observed (Angilletta et al. 2002,

Chown and Terblanche 2007). Severe temperature fluctuations and periods of extremely warm temperatures, if they exceed an organism's thermal tolerances, may lead to accumulation of physiological and/or developmental damage, which can lead to delayed or immediate mortality (Bensadia et al. 2006, Chown and Terblanche 2007, Hazell et al. 2010).

In biological communities, the effects of temperature on multiple populations depend, in part, on the individual, species-specific responses to temperatures (Angilletta et al. 2002). Even in communities where interacting species are closely linked through their life histories, such as parasitoids and their hosts, organisms may not have the same optimal temperature ranges, development curves, and upper thermal tolerances (Davis et al. 2006, Zamani et al. 2007). In relatively well-studied systems, such as aphid-parasitoid communities, the effects of temperature on individual species are well-documented. This allows us to ask how increasing and fluctuating temperatures will influence the interactions between the organisms and the overall population dynamics? Even in these systems, however, there are still many uncertainties as to which processes and interactions are important in structuring each population and in determining overall population dynamics.

Severe fluctuating temperatures may not equally affect all individuals in a population, particularly if there are multiple age classes or morphotypes. The most obvious distinction in age class is between juvenile and adult age classes. In hemimetabolous insects each age class differs in size, and in holometabolous insects, the age classes differ in both size and morphology. In summer aphid populations, juvenile and adults experience similar environmental conditions, but instars (which are smaller),

are likely more susceptible to temperature-induced mortality than adult aphids (Roitberg and Myers 1979). Aphid juveniles may also differ from each other in their propensity to develop wings and thus to generate both winged (alate) and wingless (apterous) adults that may also differ in a suite of life history traits including size, fecundity and longevity. Adult and juvenile aphids also differ in their anti-predator responses to parasitoids (Roitberg and Myers 1979, Gerling et al. 1990). Extreme and fluctuating temperatures might also influence these responses, and this could indirectly influence their subsequent mortality rates. Aphid parasitoids are koinobionts, therefore adults and juveniles face substantially different challenges in dealing with ambient temperature conditions. Juvenile parasitoids have a restricted capacity for movement which renders them incapable of modifying the environmental conditions in which they must develop (Hance et al. 2007). They are constrained to experience their host's thermal stress as well as their own thermal stress in order to successfully complete development (Hance et al. 2007). By contrast, adult parasitoids are capable of behaviourally thermoregulating by choosing where to rest, and where and when they forage for hosts.

Interactions between parasitoids and hosts can strongly influence how climate change affects organisms, and as such, must be considered when assessing the overall impacts of climate change at the community level (Davis et al. 1998, Gilman et al. 2010, Van der Putten et al. 2010). Parasitoids directly and indirectly impact their hosts through lethal and non-lethal effects, and hosts can directly and indirectly impact the parasitoid through host quality, size and anti-predator defenses (Müller and Godfray 1999, Villagra et al. 2002, Henry et al. 2010, Thomson et al. 2010). Furthermore, as noted above, such impacts can vary across stages or morphotypes. Although not all interactions may alter

population dynamics, the impacts of temperature on these interactions should be assessed when attempting to determine the effects of climate change in a community context.

I explored how maximum daily temperatures (which also increases the amplitude of daily temperature fluctuations), the frequency of warmer-than-average days, and the autocorrelation of those warm days, impact host-parasitoid population dynamics in an aphid-parasitoid system. To do this I constructed a stage-structured Leslie matrix model with intra-generational dynamics incorporating individual behaviour (e.g. stage-dependent escape responses). I included stage-structure and distinguished the aphid populations by their functional forms (alates and apterae) so that I could also explore the effect of different sensitivities to temperature based on age class and to include additional biologically realistic information to imitate the intra-generational processes contributing to the overall host-parasitoid population dynamics.

2.3 Methods

2.3.1 Model Formulation

I constructed a stage-based, Leslie projection matrix where development, reproduction, and mortality are functions of temperature (Figure 1). The model was constrained to a single continuous 'patch' and therefore included no metapopulation dynamics. Intra-generational dynamics were considered and one hour time steps were used because the temperature determination function generated hourly temperatures. The transition functions were deterministic, but there was stochasticity in the temperature determination function. The stochasticity was controlled by drawing temperatures from the same distribution for generation of all temperature profiles. Aphid and parasitoid

population dynamics were examined over a 150 day period to approximate a summer growing season at temperate latitudes.

The parasitoid population was separated into two stages: juvenile (egg, larva, pupae) and adult. Alate and apterous aphid populations were tracked separately, and like the parasitoid population, the alate and apterous aphid populations were separated by age class into five stages (1^{st}, 2^{nd}, 3^{rd}, 4^{th} instar and adult). The sets of equations and associated functions that describe the aphid and parasitoid populations are described in Appendix A.

2.3.2 Temperature determination

Temperature profiles were produced using a stochastic sinusoidal model designed for modelling temperature in an agricultural setting (Eq. 1) (De Wit 1978, Wann et al. 1985).

$$T_{(t)} = \begin{cases} \frac{1}{2}(T_{\max} + T_{\min}) - \frac{1}{2}(T_{\max} - T_{\min}) \times \cos\left(\frac{\pi(t - t_{\min})}{(t_{\max} - t_{\min})}\right) & t_{\min} \le t \le t_{\max}; \\ \frac{1}{2}(T_{\max} + T_{\min'}) + \frac{1}{2}(T_{\max} - T_{\min'}) \times \cos\left(\frac{\pi(t - t_{\min})}{24 - (t_{\max} + t_{\min'})}\right) & t_{\min} \le t \le \mathrm{t}_{\max}; \end{cases} \quad (1)$$

T_{max} was the maximum temperature of the first day, and T_{min} was the minimum temperature for the first day, $T_{max'}$ was the maximum temperature of the following day and $T_{min'}$ was the minimum temperature of the following day.

$T_{min'}$ and $T_{max'}$ for each subsequent day were generated by drawing numbers from a beta distribution which was modified by the range of maximum daily temperatures T_{range}, the frequency of warmer-than-average days b, and the autocorrelation of the daily

temperatures *q* using R 2.11.1 (R Development Core Team 2010). I used three maximum daily temperature ranges, three frequencies of warmer-than-average daily maximum temperatures, and three levels of autocorrelation (Table 1) in a factorial design to generate twenty-seven unique temperature profiles. The temperature profiles were then used to examine the effects of extreme and fluctuating temperatures on aphid-parasitoid community dynamics. Figures 2, 3, and 4 depict the minimum and maximum daily temperatures for all twenty-seven temperature profiles.

2.3.3 Model parameterization

The model used parameters that approximately describe *Aphidius matricariae* (Hymenoptera: Braconidae) foraging on green peach aphids, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). Aphid and parasitoid growth rates, aphid reproductive rates, and parasitoid foraging preferences were taken from the literature where available. The values for all model parameters are included in Table B-1 in Appendix B.

The aphid development rates in fluctuating environments were based on the results of Liu & Meng (1999). Maximum development rate occurred at 28 °C. Liu & Meng (1999) also noted that alate development times were 1.14 times higher than those of apterous individuals so that was reflected in the parameter values. Under constant ideal conditions for growth, an apterous aphid will reach maturity in 5.5 days, but under fluctuating temperatures the optimum development rate is likely different (Davis et al. 2006).

Reproductive rates for the apterous aphids were taken from (Satar et al. 2008). Reproductive rates for the alate aphids were half of the reproductive rates for the apterous aphids (Noda 1960, Dixon and Wratten 1971). Under constant ideal conditions, apterous

aphids could produce eight offspring per day although realized reproductive rates were much lower due to the daily temperature cycling. Although adult aphids do not have uniform fecundity across their entire life span (Satar et al. 2008), I did not explicitly model age specific fecundity. The ideal temperature for reproduction was 27 °C (Davis et al. 2006). At aphid densities above approximately 12,000 total aphids reproductive rates decrease based on the density dependent growth term in the *m* function. At approximately 20,000 aphids, reproduction was zero.

The production of alate aphids was also density dependent and was induced when crowding occurred in the model. The generation of alates is known to be induced through increased contact with other individuals (Wadley 1923, Sutherland and Mittler 1971, Muller et al. 2001). Although temperature may influence alate production (Gillespie et al. 2011) I did not include it since there were no published estimates of the effects of temperature on rates of production of alates. I constrained the population so that the maximum proportion of alates produced was 50% of the reproduction per time step.

Parasitoid development rates were taken from Zamanii et al (2007) for *Aphidius matricariae* developing on *M. persicae*. Under ideal constant temperature conditions (27 °C) *A. matricariae* can reach maturity in 11.5 days. Realized development times were likely substantially longer, due to limited time spent at optimum temperatures on a daily basis.

Parasitoid foraging speed T_{maxs}, measured as the area searched per time step, and was highest at temperatures between 25 and 30 °C (Zamani et al. 2006). The actual maximum area covered per one hour time step *v* was 3.3% of the total area of the 'patch'.

This value was not directly available in the literature thus it was varied between 1 and 7 % and evaluated it in the sensitivity analysis.

The functional response of the parasitoid encompassed both consumptive and non-consumptive effects. It was modelled to incorporate preferences and success rates for different age classes of aphids. Aphid parasitoids generally prefer younger instars, but the preference depends on the parasitoid and aphid species as well as the size of the aphids (Tahriri et al. 2007). I included a preference for juvenile aphids, but did not include preferences between the four juvenile instars or between alate and apterous individuals. The handling time was divided into two values: time spent assessing the host's suitability *thp*; and time spent ovipositing into the host *tha*. I assumed a single assessment time across aphid age classes; however, different times spent ovipositing were defined since there is evidence of instar-specific defensive behaviours as aphids progress to older instars (Gerling et al. 1990). The time spent ovipositing into hosts was twice as long (10 seconds) for adult aphids relative to the time spent ovipositing into juvenile aphids since adult aphids defensive behaviours are more difficult to overcome for the parasitoids. I did not distinguish assessment time between different juvenile instars; rather I assigned a similar 'average' value. The probability of successfully attacking an aphid μ after the parasitoid accepts that host may also differ based on age class (Gerling et al. 1990). There was uncertainty as to the true values or distributions of values associated with the parameters that describe the parasitoid's functional responses. The impacts of these parameters were assessed in my sensitivity analysis.

Mortality of the aphids and parasitoids came from three sources: background mortality ζ, senescence γ, and temperature. Aphids were also be killed through

parastitism $n_{i,w}$. The background mortality rates included mortality due to random chance and did not include sources of mortality such as predation. Background mortality was 2% per day for the aphids and 4% per day for the parasitoids. Mortality from senescence γ was included to ensure adult aphids and parasitoids were constrained to realistic adult life-spans. For adult aphids, γ was set so that the maximum adult lifespan was 14 days. For adult parasitoids, γ was set so that the maximum adult lifespan was 10 days. Temperature dependent mortality increased exponentially as temperatures approached the organism's upper thermal tolerance. The absolute and relative values of this parameter are critically important when examining the effects of temperature on overall population dynamics. Although described in terms of an actual temperature, T_{maxd} was not derived directly from real values; rather it was determined through sensitivity analysis; mortality rates at high temperatures were biologically reasonable and1 hour of exposure to 40 ° C resulted in ~10% mortality in both aphids and parasitoids. The slope of the mortality curve was determined by ψ, decreasing the value of ψ increased temperature dependent mortality across all temperatures. By modifying the absolute values of ψ for aphids and parasitoids, and the relative values of ψ based on age class I explored how this parameter influenced population dynamics and population persistence.

There was limited information regarding the effects of high temperature on aphid mortality in different age classes (Asin and Pons 2001, Hazell et al. 2010). Rather than including the parameters associated with temperature dependent mortality in our sensitivity analysis, I examined the effects of differential susceptibility to temperature-dependent mortality based on age class by comparing two versions of our model. First the model was parameterized without distinguishing the effects of temperature on the

different instars and morphologies. In this version ψ was 0.4 for all aphid age classes. In the second version, I explored the effects of including age-class specific temperature-dependent mortality rates, by increasing the susceptibility of juvenile aphids to temperature dependent mortality. I first assessed the effect of increasing mortality rates for all juvenile age classes similarly (ψ = 0.35), and then assessed the impact of further distinguishing mortality rates for each age class so that the youngest aphids experienced the highest mortality rates (ψ = 0.30 for first instar, ψ = 0.325 for second instar, ψ = 0.35 for third instar, ψ = 0.375 for fourth instar, ψ = 0.4 for adult).

I used an initial aphid population that approximated the numbers and age class distribution of an established, but exponentially-increasing, early-season population. A small number of adult female parasitoids then 'located' the patch. This simulated a scenario whereby a previously unexploited patch of aphids is located by a number of actively searching adult wasps early in the summer. The effect of starting populations was explored in the sensitivity analysis.

2.3.4 Model analysis

I first assessed the model to determine if the level of stage-structure was justified. A number of parameters could differ based on age class for the aphid and parasitoid populations. Many of the parameters used to describe the parasitoids' functional response could differ based on aphid age class including the probability of a parasitoid successfully attacking it's host, the maximum area covered of a foraging wasp per time step, the probability of rejecting a host, the handling time of assessment, and the handling time of attack. Mortality due to temperature can also differ based on age class. I compared the extinction times and population persistence results of my model which

included different parameter values for each age class specifically to a second model that employed parameters with single values from averaging across all age classes and using that value to describe all age classes effectively removing age structure from our model.

A sensitivity analysis was performed to determine which parameters had the greatest influence on aphid-parasitoid community dynamics in terms of population persistence (Table 2-2). Population persistence was measured as the number of temperature regimes in which the aphids were not driven extinct after 150 days, and the time to extinction for those populations that were driven extinct before 150 days. In all cases, I constrained the sensitivity analysis to parameter values that were biologically realistic. Of the parameters that were not drawn from the literature, the parameters that had the largest impact on community dynamics were the background mortality levels ζ, the probability of successfully attacking an aphid μ, and the time spent assessing the host's suitability *thp*. Other parameters had minimal effects on the community dynamics in terms of population persistence and therefore are not discussed further in the results section. The parameters which had minimal community level effects includes: the area covered by a searching parasitoid v, the parasitoid instar preference ε, the total proportion of alate offspring that can be produced α, the time spent ovipositing into the host *tha*, the aphid and parasitoid mortality due to senescence γ, the relative contribution to reproduction from apterous and alate adults κ, the slope of the development curve ω when temperatures exceed T_{maxg}, the slope of the aphid reproduction curve ξ when temperature exceed T_{maxb}, and the slope of the parasitoid foraging speed curve ι when temperatures exceed T_{maxs}. The effects of initial population size and the seed number used to generate the temperature profiles were also explored in the sensitivity analysis.

The seed number corresponds to the set of random numbers used to generate the temperature profiles. A regression of timing of the first very warm day and the subsequent extinction times was performed to examine the effect of seed number on community dynamics using JMP 8.02 (SAS-Institute 2009).

After assessing the model's sensitivity to uncertain parameters and initial population size I examined how the amplitude, frequency and autocorrelation of temperature regimes influenced aphid and parasitoid population dynamics. Then, I examined how the amplitude, frequency and autocorrelation of temperature regimes influenced aphid and parasitoid population dynamics when I included differential susceptibility to temperature dependent mortality based on aphid age class (instar). In all cases, I assessed the impact of temperature on community persistence, and time to extinction for those communities driven extinct prior to the end of the 150 day simulation.

2.4 Results

2.4.1 Stage-structure

Including age-class-specific values for the parameters associated with the parasitoid's functional response did not influence community persistence compared to a simplified version where the same mean parameter values were assigned to all age classes. Including age-class-specific values did result in increased average extinction times by up to 10 days for the apterous aphid populations however (Table 2-3). Age-class-specific mortality of aphids due to temperature did influence community persistence and is explored in more detail below.

2.4.2 Parameter estimation

Some parameters were not derived from previous studies and I was uncertain as to their true value. I performed a sensitivity analysis to determine how the values of the uncertain parameters influenced community persistence. For the set of parameters that was used for the actual model analysis, without differential temperature dependent mortality based on age class, twelve of the twenty-seven temperature regimes had persistent communities after 150 days (Figures 5-7). Here I focused on the parameters that had qualitative or substantial quantitative effects on the community persistence and also note when there are effects on population sizes.

Background mortality levels ζ of both the aphids and the parasitoids influenced population numbers and population persistence. The background mortality rate for the aphids produced 2% mortality per day for the aphids and 4% for the parasitoids. Doubling the background mortality of the aphids resulted in decreased extinction times, and one additional community went extinct. Halving the background mortality of the aphids resulted in one additional temperature regime with persistent populations, and increased the time to extinction in the other temperature regimes where the populations went extinct prior to the 150 day simulations ended. Doubling and halving the background mortality of the parasitoids resulted in a decrease and increase, respectively in parasitoid population size, but had no impact on community persistence.

Two of the parameters related to the wasp's functional response affected community persistence. Increasing the probability of successfully attacking an aphid μ from 40% to 60% decreased the extinction times but did not impact the persistence of the communities. Reducing the probability to 20% from 40% increased extinction times in populations that did not persist beyond 150 days, but no additional communities went

extinct. The time spent assessing the host's suitability *thp* influenced parasitoid population sizes and community persistence. Increasing the time spent assessing the host's suitability by 20 seconds to 60 seconds resulted lower parasitoid populations, and increased extinction times. One additional community that previously went extinct, persisted over the 150 day timeframe (intermediate amplitude, high frequency, low autocorrelation temperature regime). Decreasing the time spent assessing the host's suitability by 20 seconds to 20 seconds increased the parasitoid populations substantially, reduced extinction times and reduced the number of temperature regimes that resulted in persistent communities to 11 from 12. *Aphidius* parasitoids are fast moving, active predators, with low assessment and oviposition times, so further increasing the time spent assessing the host's suitability beyond the range that was explored is not consistent with the biology of the species.

Initial size of the aphid and parasitoid populations did not have a large effect on the model results. Initial aphid populations between 3,000 and 15,000 produced similar overall results with respect to community persistence across the range of temperatures. This is the range of population sizes where the aphid population is already growing at a high rate. The number of adult aphids did not impact overall dynamics if starting aphid population was held constant. The absolute number of alate aphids and the relative number of alate aphids to apterous aphids did not influence the overall model results. Initially only a small number of adult parasitoids were introduced into the model. Increasing the number of adult parasitoids while holding the initial aphid population constant did not change the overall results. After assessing the effect of initial population

size, 7500 aphids, with 15% of the population alate individuals and 85% of the population apterous individuals was used as the initial population size for the model.

The function used to generate the daily minimum and maximum temperatures of the next day ($T_{min'}$ and $T_{max'}$) was stochastic, and therefore the seed number of the beta distribution influenced the temperature profiles. Changing the seed number did not dramatically alter the results of the model, except in three of the temperature profiles. Under high amplitude (T_{range}) and low frequency (b) conditions the community dynamics in the three regimes that differed based on their autocorrelation (q) (Figure 7 column 1) were sensitive to the timing of days which had maximum daily temperatures above the organisms thermal tolerances. The extinction times of the communities varied depending on seed number, by as much as 80 days. The temperature regimes with low and intermediate levels of autocorrelation always resulted in extinction, but the high autocorrelation temperature regime occasionally persisted beyond 150 days. There appears to be a relationship between the timing of the days that exceed the organisms' thermal tolerances and the autocorrelation of the warm days. A regression of extinction time in response to the timing of the first day where the maximum temperature was above 35 C indicates that the timing of the first hot event influenced extinction times (Regression, $F\text{-ratio}_{1,13} = 9.5$, $r^2 = 0.42$, $p = 0.009$).

Overall most of the parameters of the model that were assessed in the sensitivity analysis had little impact on the conclusions regarding the effects of extreme and fluctuating temperature regimes on the communities in the model.

2.4.3 Overall model

I examined the effects of the amplitude, frequency, and autocorrelation of the temperature regimes on aphid and parasitoid population persistence and time to extinction. Figures 5, 6 and 7 plot the apterous, alate, and parasitoid populations over time based on the temperature regime without differential temperature dependent mortality based on age class (ψ = 0.4 for all age classes). In populations that went extinct, the alate aphid population was the first population driven to extinction, the apterous aphids were second, and the parasitoids were the last driven to extinction. I used the time to extinction for the apterous aphid populations as the measure of time to extinction rather than citing three correlated values.

2.4.4 Identical temperature dependent mortality based on age class

Increasing the amplitude of maximum daily temperatures (T_{range}) resulted in increased extinction (compare Figure 5, 6 and 7). Temperature regimes in which the daily temperatures were constrained to fluctuate between 10 and 30 °C (daily maximum temperature between 20 and 30°C) resulted in persistent aphid and parasitoid populations irrespective of the frequency of warmer-than-average days or the autocorrelation of the daily temperatures (Figure 5). Population fluctuations increased with increasing amplitude and when combined with an increase in the frequency of warmer-than-average days community extinction occurred (Figure 6). All communities were driven extinct within 150 days in the temperature regimes with high amplitudes. The times to extinction at high amplitudes varied depending on the frequency of warm days and on autocorrelation (Figure 7).

Increasing the frequency of warmer-than-average days *b* did not impact community persistence under low amplitude T_{range} regimes since the warmer-than-average days failed to reach temperatures at which temperature-dependent mortality was a significant factor (Figure 5). Increasing the frequency of warm days at intermediate and high amplitudes resulted in increased community extinction (Figure 6, 7).

The effect of increasing the autocorrelation of daily maximum and minimum temperatures *q* was dependent on the amplitude and frequency of warmer-than average-days (Figure 6). Increasing autocorrelation produced fewer warm periods during the simulation, but increased the length of those hot periods producing 'heat waves' rather than periodic warm days throughout the simulation. Population fluctuation, measured by comparing the number times the populations growth shifted from positive to negative, decreased with increasing autocorrelation under a low frequency of warm days at intermediate temperatures. The time to extinction increased with increasing autocorrelation and increasing frequency of warm days. When the amplitudes are high (Figure 7) a similar trend is observed. Population persistence increases with increasing autocorrelation if the frequency of warm days is low, but decreases with increasing autocorrelation at intermediate and high frequencies of warm days. The combined effects of all three temperature parameters on community persistence and time to extinction are summarized in figure 8.

2.4.5 Differential temperature dependent mortality based on age class

If I increased juvenile aphid mortality due to temperature relative to the mortality of the adult aphids (ψ = 3.5 1st instar, ψ = 3.5 2nd instar, ψ = 3.5 3rd instar, ψ = 3.5 4th instar, ψ = 4.0 adult), the model results were qualitatively similar to the model without

differential mortality (ψ = 4.0 1st instar, ψ = 4.0 2nd instar, ψ = 4.0 3rd instar, ψ = 4.0 4th instar, ψ = 4.0 adult) (compare Figure 8 and 9). Increased amplitude and frequency reduced community persistence, and the effect of increased autocorrelation depended on whether the population was persistent or not. Under low amplitude fluctuations there were no changes to the persistence of the communities compared to the model that treated all aphid age classes similarly in relation to temperature dependent mortality. In all cases where extinction occurred when mortality for all age classes was identical, differential mortality of juveniles reduced extinction times by as much as 56 days.

Progressing a step further and assigning instar specific mortality rates based on temperature (ψ = 3.0 1st instar, ψ = 3.25 2nd instar, ψ = 3.5 3rd instar, ψ = 3.75 4th instar, ψ = 4.0 adult), which likely is the most realistic in terms of real aphid populations, produces further extinction. Sufficient additional mortality was introduced to drive one additional community extinct (intermediate amplitude, low frequency, low autocorrelation), and close to driving a second extinct (intermediate amplitude, low frequency, high autocorrelation) (Figure 6). For the communities that were driven to extinction, the extinction times were further decreased by adding this additional mortality (compare Figure 9 and Figure 10).

2.5 Discussion

2.5.1 Model evaluation

Matrix models have been used extensively to model populations, and are particularly useful to describe populations that have a distinct stage-structure, such as the aphid and parasitoid populations (Birt et al. 2009). I used a stage-structured model to explore the effects of extreme and fluctuating temperatures on an aphid-parasitoid

community because there was evidence indicating that all age classes or life-history stages of the focal organisms were not equally impacted by extreme and fluctuating temperatures (Roitberg and Myers 1979).

Initially, I parameterized the functions that described the aphid populations by instar, attributing different values to each instar, based on extrapolation from values reported in the literature. In most cases, this level of detail proved unnecessary since using the average value for all aphid age classes resulted in the same overall dynamics and community persistence. This was also the case for parameters describing parasitoid oviposition preference and success, and parasitoid handling times.

The model was insensitive to parameters associated with the parasitoid functional response in terms of community persistence. Using the average value applied to all of the instars resulted qualitatively in similar results. This agrees with Mondor and Roitberg (2000) who concluded that variance in host selection does not impact dynamics greatly, at least within a Nicolson-Bailey framework. Although interactions between organisms are important, modelling explicit behavioural mechanisms may be unnecessary if the goal of the model is to characterize the overall population and community level effects.

Although aphid stage-structure was not necessary to describe the wasp's functional response, it was still useful to use stage-structure to distinguish the immature and adult stages of the aphid and the parasitoid populations. When modelling intra-generational dynamics, the distinction between adult and juvenile individuals was necessary to properly describe how each class interacts with temperature and with other populations. Additionally, separating the alate and apterous aphid populations allowed me to more accurately model aphid reproduction and development since reproductive and

developmental rates differ between the two morphs (Noda 1960, Dixon and Wratten 1971, Liu and Meng 1999).

Incorporating additional biologically-realistic parameterization based on evidence that younger age classes of aphids are more susceptible to temperature induced mortality, I found age-class-specific temperature dependent mortality influenced extinction time and community persistence under several temperature regimes (Figure 8, 9 and 10). This highlights a situation where calculating the mean value for a parameter and then attributing that value to multiple age classes fails to produce the same results compared to attributing age-class specific values to each age class. For key model parameters, it should not be assumed that simple averages are always adequate to describe the complex interactions between organisms and the ambient environment.

2.5.2 Community level impacts of extreme fluctuating temperatures

The model results suggest that the maximum daily temperatures (amplitude), the frequency of warmer-than-average days, and the autocorrelation of extreme temperature events can all impact population dynamics of ectothermic species. However, the overall impact that these three phenomena had on communities was not independent. Whether daily temperatures exceeded the thermal tolerances of one or more of the organisms appeared to be a key factor in determining the effects of the frequency and autocorrelation of warm days. When daily maximum temperatures were below the organisms' maximum thermal tolerances (low amplitude), additional temperature phenomena such as the frequency of warmer-than-average days or the stability of day to day temperatures had little to no impact on the persistence of the communities or the size of the populations. Increasing the amplitude, which produced daily temperatures that

exceeded the upper thermal tolerances of one or more of the organisms in the community, negatively influenced the populations directly resulting in an increased chance at community extinction. Increased amplitude indirectly increased the impact that both an increased frequency of warm days and increased autocorrelation of daily temperatures had on the overall community dynamics.

These results suggest that the frequency and autocorrelation of warm temperature events may only lead to negative community level effects when ambient temperatures are extremely warm. More frequent severe periods with extreme warm daily temperatures are predicted under climate-change models (Easterling et al. 2000, Meehl and Tebaldi 2004), so the frequency and autocorrelation of these events may be important to accurately assess how temperatures are influencing community dynamics.

Here, I examined extreme fluctuating temperatures theoretically, but some experimental work focusing on the same temperature phenomena was recently completed. Gillespie et al. (2011) experimentally examined the effects of the amplitude and frequency of daily temperatures on communities of *M. persicae* and *A. matricariae* on pepper plants, which are the same species that I modelled here. They found effects at all three trophic levels but little evidence for effects of temperature on the trophic cascade; probably because the impact at each trophic level had the potential to cancel out effects at higher levels of interaction. Although this study did not examine the basal trophic level I did observe similar negative effects that high amplitudes and frequency had on the second and third trophic levels. A natural extension to my current model would include the basal trophic level, since it can also be influenced by the same temperature phenomena. Other than temperatures, the conditions which my 'aphids'

developed under were ideal. Under less than ideal conditions, for example, if extreme fluctuating temperatures led to a reduction in primary productivity and limited the growth rates of the organisms occupying the first trophic level, then there may be additional negative impacts in the second and third trophic levels.

Although there are large scale studies examining the overall effects of climate change on communities (Hulle et al. 2010, for example), and studies examining a single populations or trophic levels (Hazell et al. 2010, for example) there has been little work that focuses on a single community. Although I parameterized my model to emulate an aphid-parasitoid community, the results in respect to how extreme fluctuating temperatures can influence community dynamics are quite general. They likely hold true for most terrestrial communities composed of multiple ectothermic species, with the nature and strength of the effects depending on the organisms' specific thermal tolerances.

2.6 Acknowledgements

I would like to thank A. Chubaty, M. Wu, and B. Ma for their generous assistance coding and troubleshooting my model. I would also like to thank Dr. Gillespie, and Dr. Cory for their input on this chapter. Funding was provided by an NSERC Strategic grant held by BDR and DRG.

2.7 Tables

Table 2-1 Temperature parameters used to generate the temperature profiles used to assess the impacts of extreme and fluctuating temperature on aphid-parasitoid population dynamics. T_{range}, b and q were combined in a factorial way to generate the twenty-seven unique profiles.

Parameter	Value		
Maximum daily temperature range (T_{range}) (°C)	Low (25 - 30 °C)	Intermediate (25 - 35 °C)	High (25 - 40 °C)
Frequency (b)	Low	Intermediate	High
Autocorrelation (q)	Low	Intermediate	High

Table 2-2 Summary of sensitivity analysis results examining how aphid and parasitoid parameter values influenced the community persistence of the communities across the 27 temperature regimes.

Parameter	Value used for model	Value tested	Effect on community persistence
ζ (aphid)	0.0004	0.0002	One additional persistent community (13 persistent)
		0.008	One additional community driven extinct (11 persistent)
ζ (parasitoid)	0.0032	0.0016	No effect
		0.0064	No effect
μ	0.4	0.2	No effect
		0.6	No effect
thp	40	20	One additional community driven extinct (11 persistent)
		60	One additional persistent community (13 persistent)
ν	0.033	0.017	No effect
		0.066	No effect
ε	0.4	0.2	No effect
		0.8	No effect
α	0.5	0.1	No effect
		0.9	No effect
tha	5	2.5	No effect
		10	No effect
γ (aphid)	0.003	0.0015	No effect
		0.006	No effect
γ (parasitoid)	0.0042	0.0021	No effect
		0.0084	No effect
κ (aphid)	0.17	0.85	No effect
		0.34	No effect
κ (parasitoid)	0.33	0.17	No effect
		0.66	No effect
ω	1.5	0.75	No effect
		3	No effect
ξ	1.5	0.75	No effect
		3	No effect
ι	1.5	0.75	No effect
		3	No effect

Table 2-3 Effect of age class specific values for parasitoid functional response on community extinction times. Note the mean extinction times do not include the communities that were persistent over the 150 day simulation. Mean parameter values: ε = 0.4, μ = 0.4, *thp* = 40.0, *tha* =5.0. Age class specific values: ε_1 = 0.5, ε_2 = 0.3, ε_3 = 0.3, ε_4 = 0.5, ε_5 = 0.6, μ_1 = 0.6, μ_2 = 0.5, μ_3 = 0.4, μ_4 = 0.3, μ_5 = 0.2, thp_1 = 20.0, thp_2 = 30.0, thp_3 = 40.0, thp_4 = 50.0, thp_5 = 60.0, tha_1 =1.0, tha_2 =3.0, tha_3 =5.0, tha_4 =7.0, tha_5 =9.0. Subscript notation indicates aphid age class (instar).

	Mean apterous aphid extinction time (Days)	
Parameter	Mean of age-class specific values applied to all age classes	Age class specific values
ε	36.4	47.0
μ	36.4	45.2
thp	36.4	40.7
tha	36.4	45.5

2.8 Figures

$$T_x \begin{bmatrix}
a_{1,1} & 0 & 0 & 0 & F_5 f_{al,al}(T,A) & 0 & 0 & 0 & 0 & F_{10} f_{al,ap}(T,A) & 0 & 0 \\
a_{2,1} & a_{2,2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & a_{3,2} & a_{3,3} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & a_{4,3} & a_{4,4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & a_{4,5} & a_{5,5} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & F_5 f_{ap,al}(T,A) & a_{6,6} & 0 & 0 & 0 & F_{10} f_{ap,ap}(T,A) & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & a_{7,6} & a_{7,7} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & a_{8,7} & a_{8,8} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & a_{9,8} & a_{9,9} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & a_{10,9} & a_{10,10} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{1,1} & F_2 f(T,A) \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{2,1} & p_{2,2}
\end{bmatrix} A_x \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \\ a_5 \\ a_6 \\ a_7 \\ a_8 \\ a_9 \\ a_{10} \\ p_1 \\ p_2 \end{bmatrix}$$

Figure 2-1 Leslie population projection matrix describing the aphid and parasitoid populations. a_1, a_2, a_3, a_4, a_5 describe the alate aphid population. a_6, a_7, a_8, a_9, a_{10} describe the apterous aphid population. p_1, p_2 describe the parasitoid population. $f_{al,ap}$ describes the number of alate offspring produced by apterous adults. $f_{al,al}$ describes the number of alate offspring produced by alate adults. $f_{ap,al}$ describes the number of apterous offspring produced by alate adults. $f_{ap,ap}$ describes the number of apterous offspring produced by apterous adults.

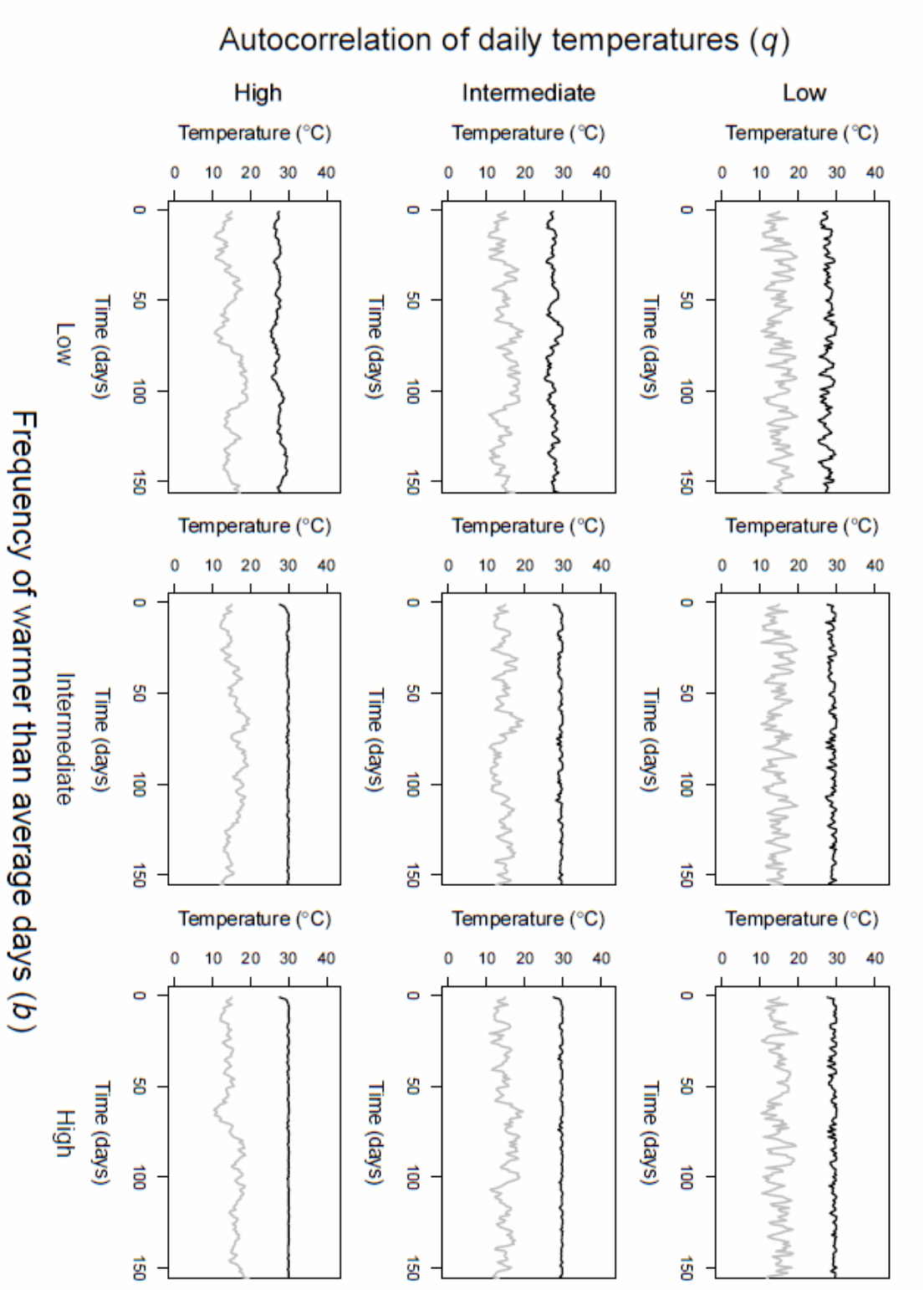

Figure 2-2 Daily minimum and maximum temperatures with low amplitude fluctuations. Daily temperatures between 10 and 30 °C.

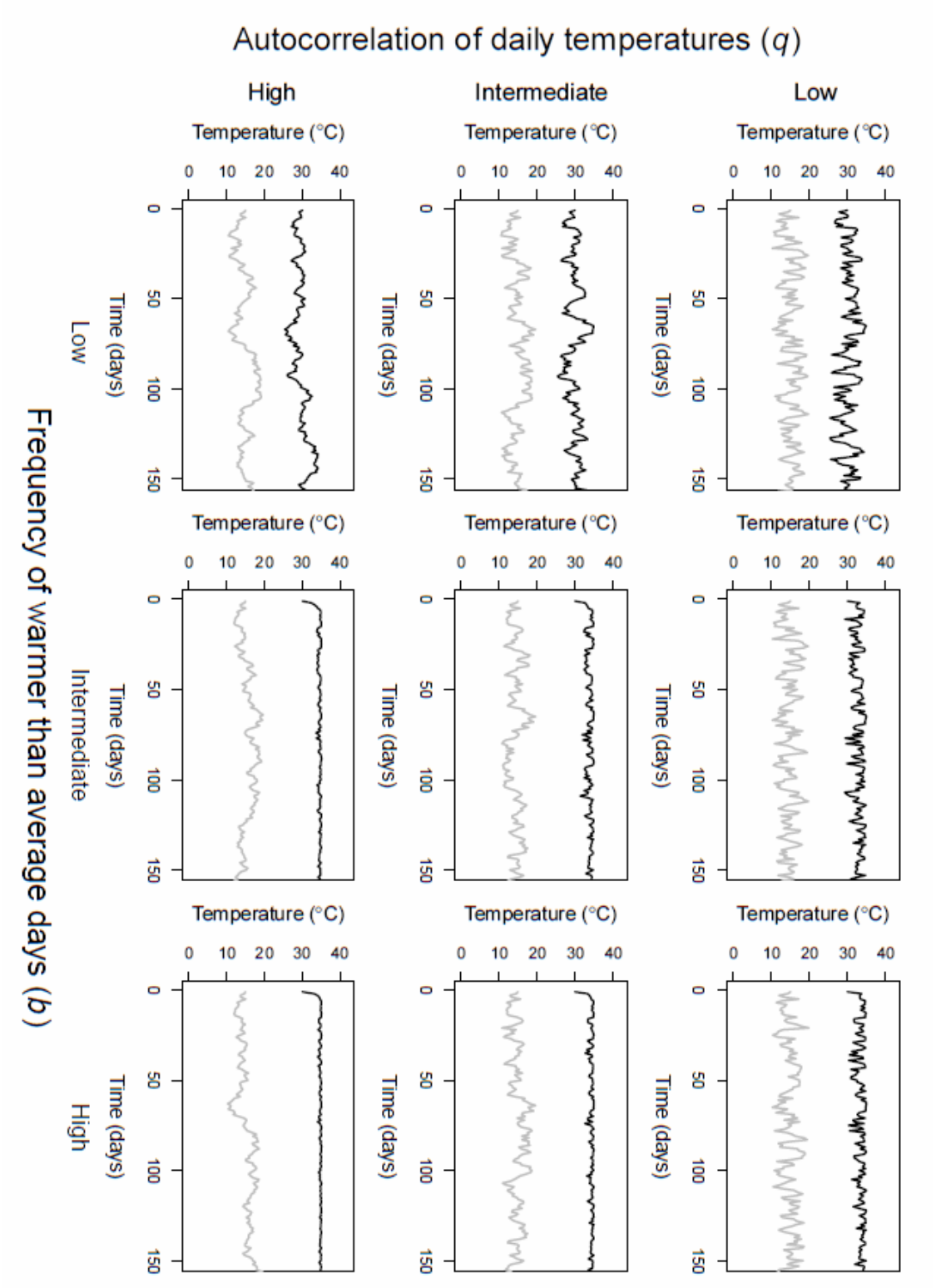

Figure 2-3 Daily minimum and maximum temperatures with intermediate amplitude fluctuations. Daily temperatures between 10 and 35 °C.

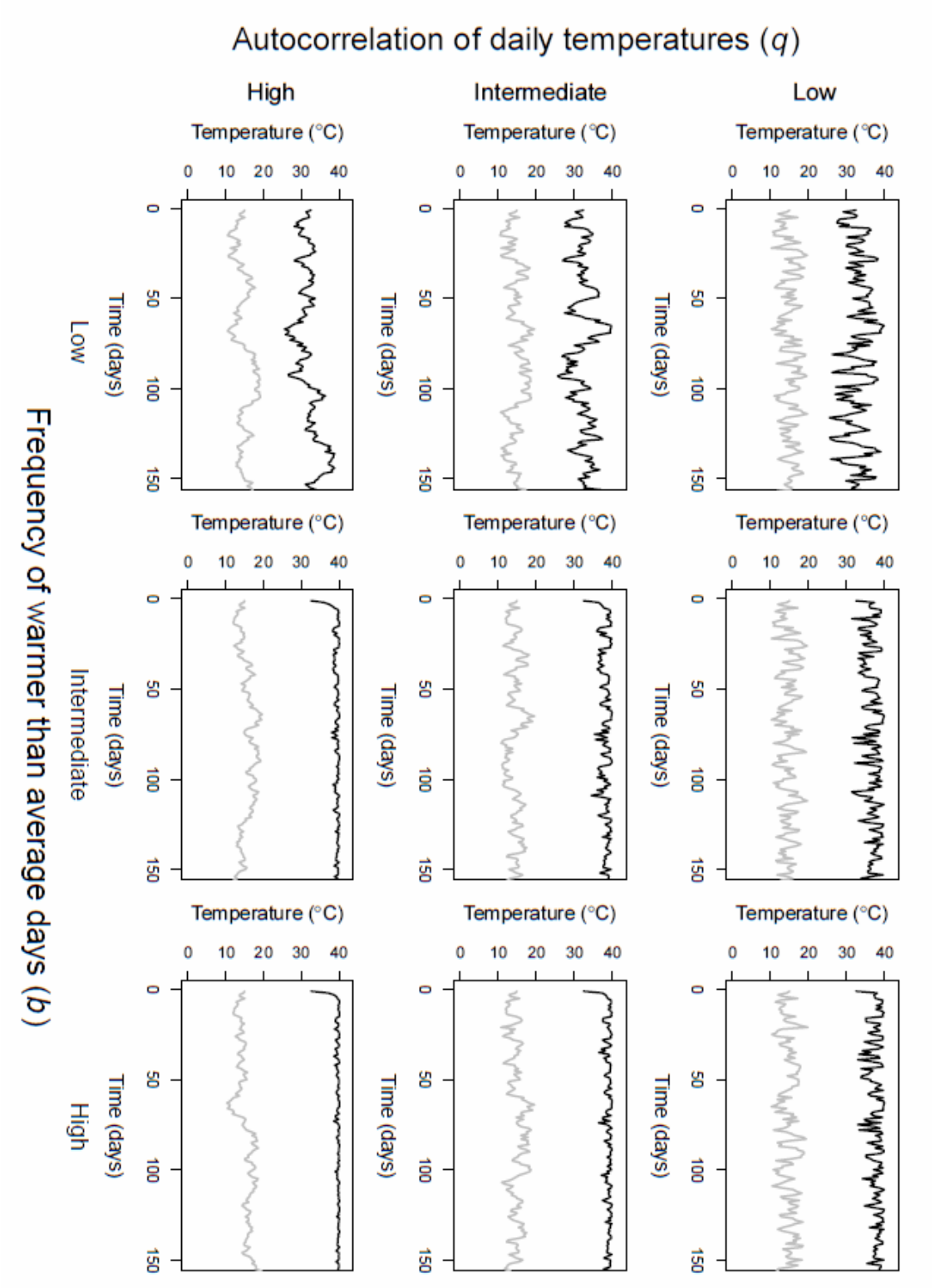

Figure 2-4 Daily minimum and maximum temperatures with high amplitude fluctuations. Daily temperatures between 10 and 40 °C.

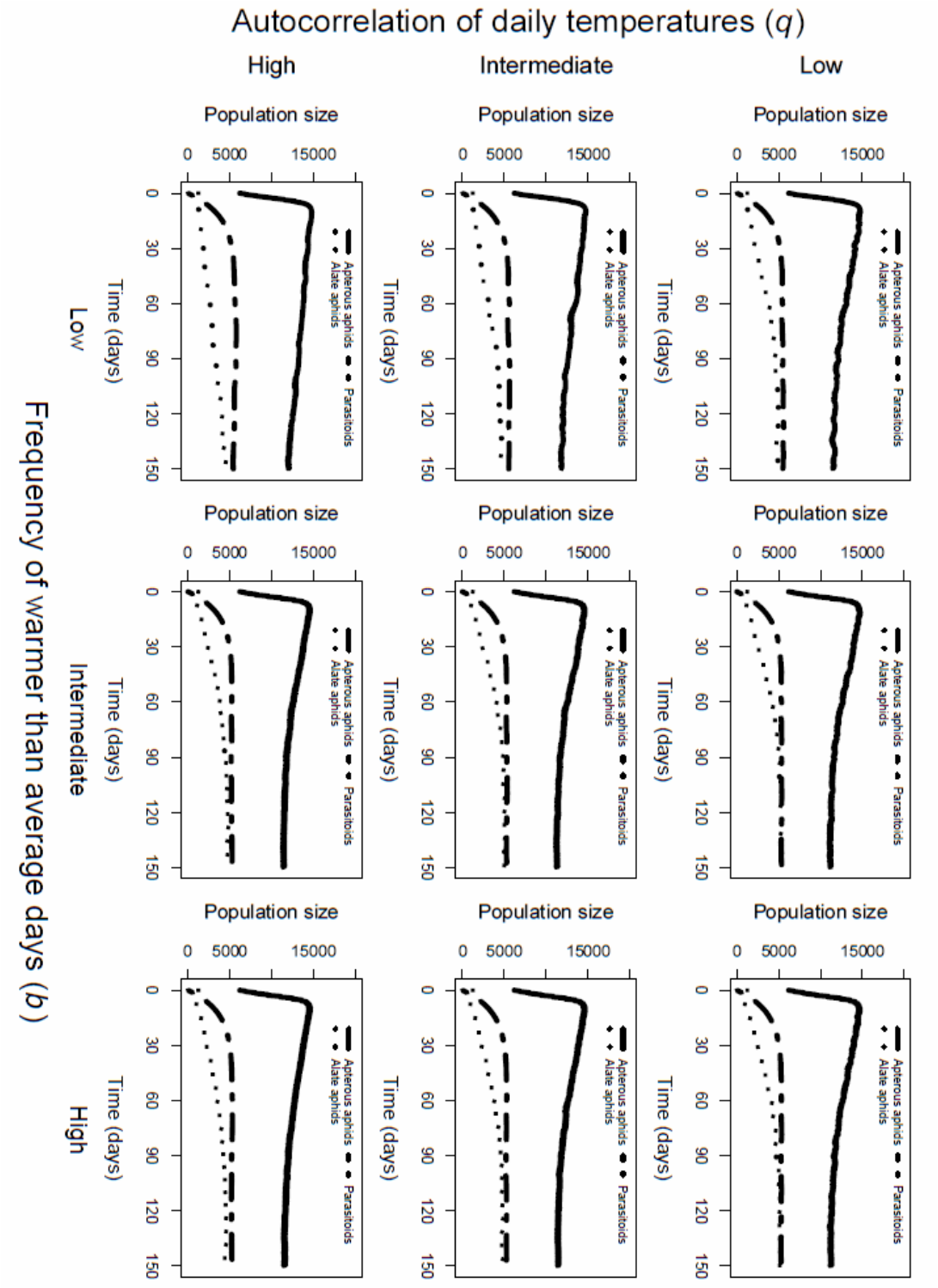

Figure 2-5 Total aphid and parasitoid populations with low amplitude fluctuations (daily temperatures between 10 and 30 °C).

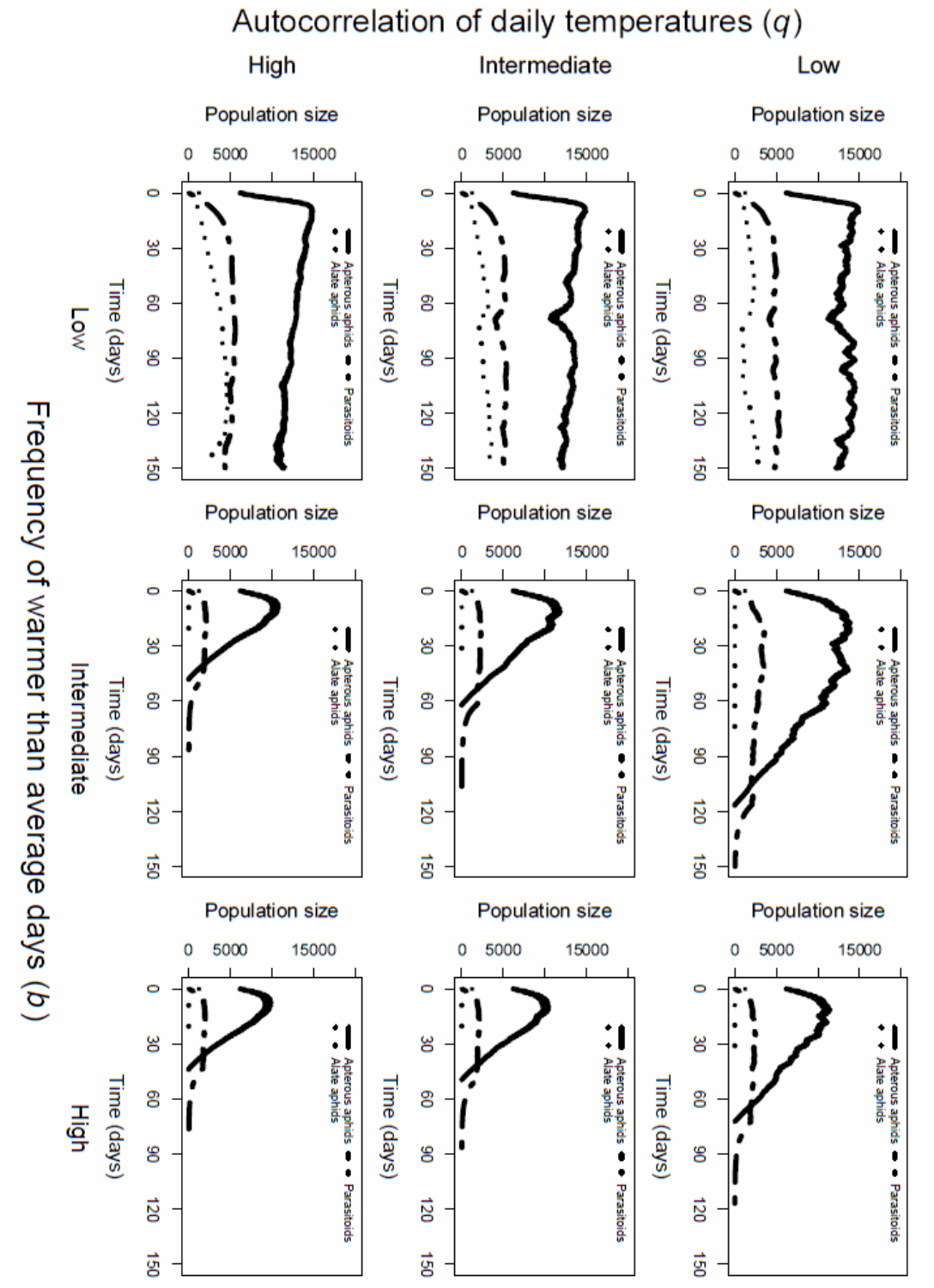

Figure 2-6 Total aphid and parasitoid populations with intermediate amplitude fluctuations (daily temperatures between 10 and 35 °C).

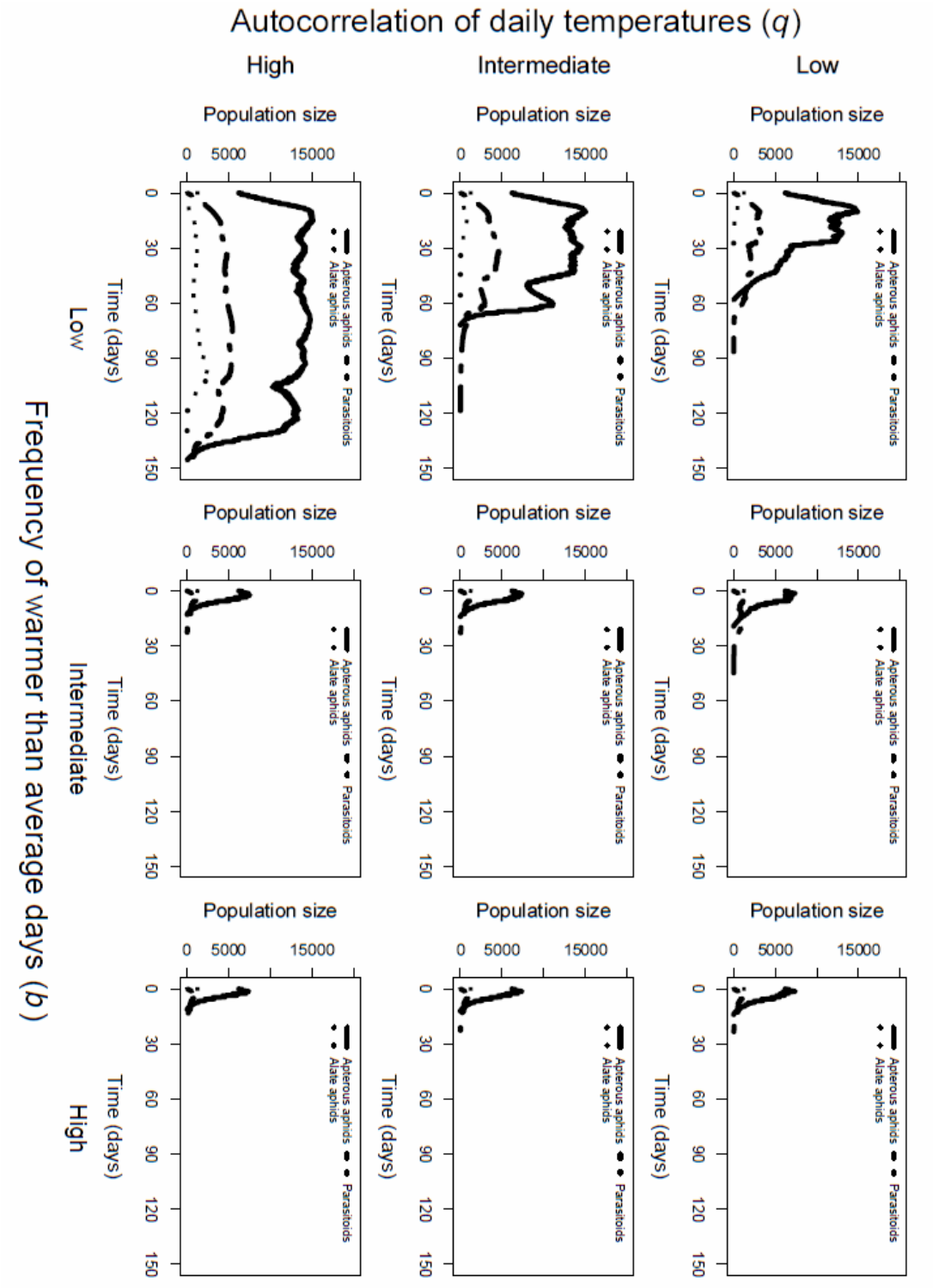

Figure 2-7 Total aphid and parasitoid populations high amplitude fluctuations (daily temperatures between 10 and 40 °C).

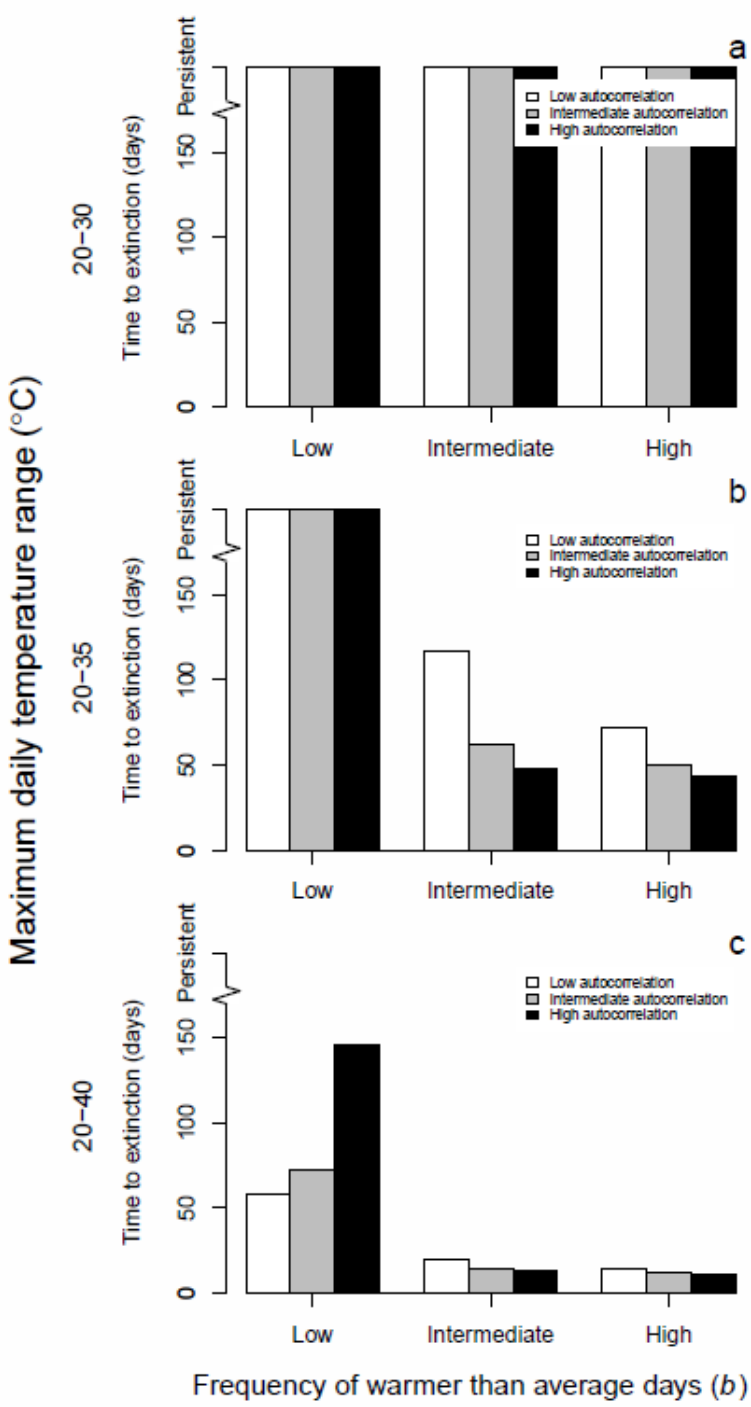

Figure 2-8 Community persistence or time to extinction depending on daily temperature range T_{range}, frequency of warm days b and the autocorrelation of daily temperatures q. All aphid age classes have the same temperature dependent mortality rates ($\psi = 4.0$ 1st instar, $\psi = 4.0$ 2nd instar, $\psi = 4.0$ 3rd instar, $\psi = 4.0$ 4th instar, $\psi = 4.0$ adult).

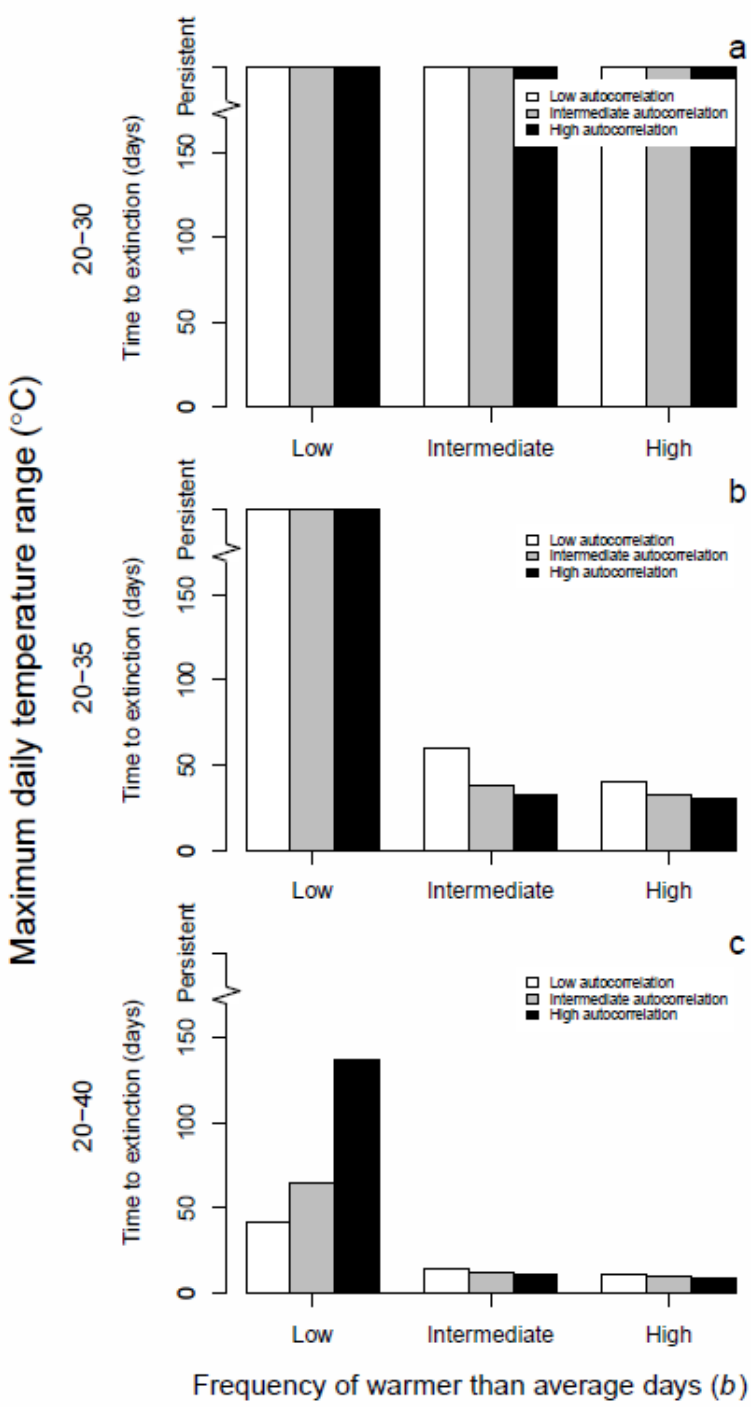

Figure 2-9 Community persistence or time to extinction depending on daily temperature range T_{range}, frequency of warm days b and the autocorrelation of daily temperatures q. All juvenile aphid age classes have higher temperature dependent mortality rates than adults ($\psi = 3.5$ 1st instar, $\psi = 3.5$ 2nd instar, $\psi = 3.5$ 3rd instar, $\psi = 3.5$ 4th instar, $\psi = 4.0$ adult).

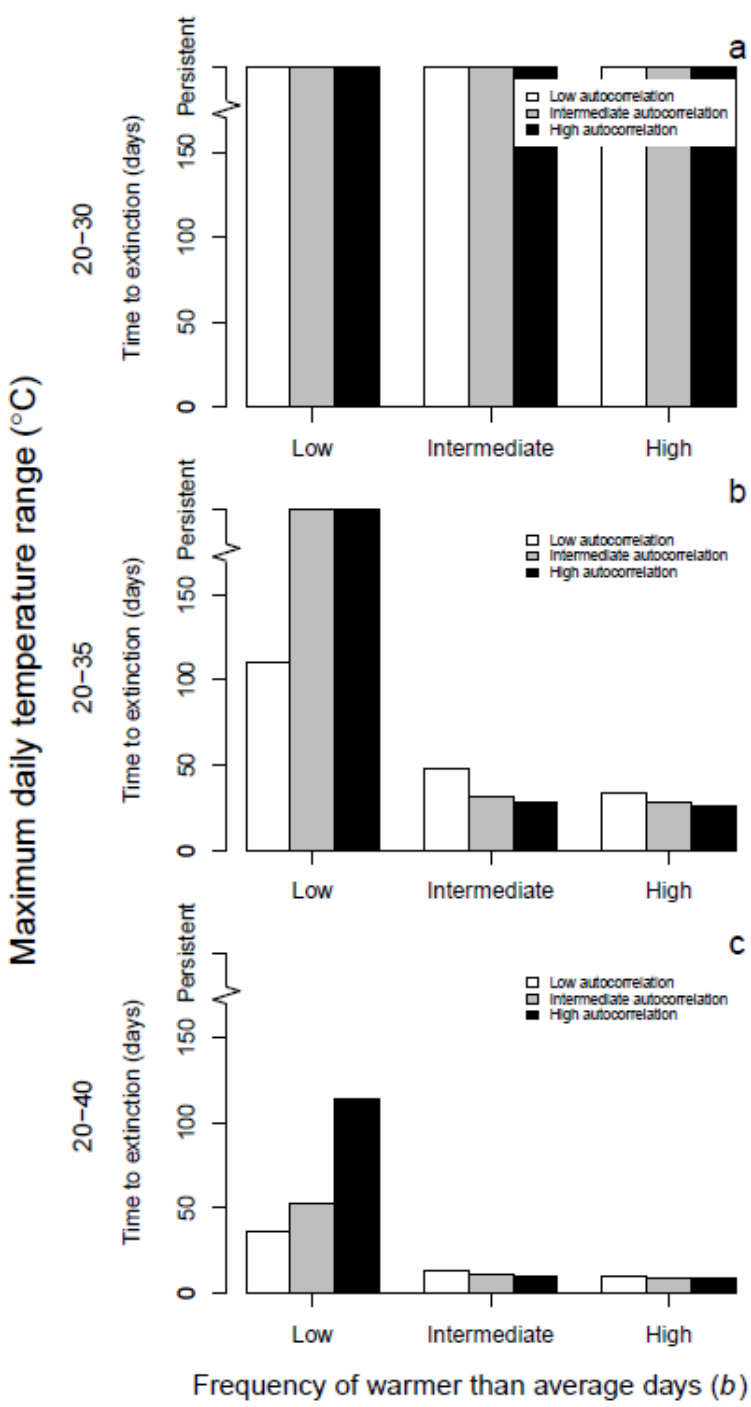

Figure 2-10 Community persistence or time to extinction depending on daily temperature range T_{range}, frequency of warm days b and the autocorrelation of daily temperatures q. Decreasing temperature dependent mortality rates based on aphid age class ($\psi = 3.0$ 1st instar, $\psi = 3.25$ 2nd instar, $\psi = 3.5$ 3rd instar, $\psi = 3.75$ 4th instar, $\psi = 4.0$ adult).

2.9 Literature cited

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology **27**:249-268.

Asin, L. and X. Pons. 2001. Effect of high temperature on the growth and reproduction of corn aphids (Homoptera: Aphididae) and implications for their population dynamics on the Northeastern Iberian Peninsula. Environmental Entomology **30**:1127-1134.

Bensadia, F., S. Boudreault, J. F. Guay, D. Michaud, and C. Cloutier. 2006. Aphid clonal resistance to a parasitoid fails under heat stress. Journal of Insect Physiology **52**:146-157.

Birt, A., R. M. Feldman, D. M. Cairns, R. N. Coulson, M. Tchakerian, W. M. Xi, and J. M. Guldin. 2009. Stage-structured matrix models for organisms with non-geometric development times. Ecology **90**:57-68.

Chown, S. L. and J. S. Terblanche. 2007. Physiological diversity in insects: Ecological and evolutionary contexts. Pages 50-152 Advances in Insect Physiology, Vol 33. Academic Press Ltd, London.

Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. Journal of Animal Ecology **67**:600-612.

Davis, J. A., E. B. Radcliffe, and R. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae). Physiological Ecology **35**:1461-1468.

De Wit, C. T. 1978. Simulation of Assimilation, Respiration and Transpiration of Crops. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Dixon, A. F. G. and S. D. Wratten. 1971. Laboratory studies on aggregation, size and fecundity in black bean aphid, *Aphis fabae* Scop. Bulletin of Entomological Research **6**:97-&.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate Extremes: Observations, Modeling, and Impacts. Science **289**:2068-2074.

Gerling, D., B. D. Roitberg, and M. Mackauer. 1990. Instar-specific defense of the pea aphid, *Acyrthosiphon pisum*: Influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelmidae). Journal of Insect Behavior **3**:501-514.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution **25**:325-331.

Hance, T., J. van Baaren, P. Vernin, and G. Boivin. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology **52**:107-126.

Hazell, S. P., B. P. Neve, C. Groutides, A. E. Douglas, T. M. Blackburn, and J. S. Bale. 2010. Hyperthermic aphids: Insights into behaviour and mortality. Journal of Insect Physiology **56**:123-131.

Henry, L. M., J. A. Bannerman, D. R. Gillespie, and B. D. Roitberg. 2010. Predator identity and the nature and strength of food web interactions Journal of Animal Ecology **79**:1164-1171

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist **91**:385–398.

Hulle, M., A. Coeur d'Acier, S. Bankhead-Dronnet, and R. Harrington. 2010. Aphids in the face of global changes. Comptes Rendus Biologies **333**:497-503.

Ives, A. R. 1995. Predicting the response of populations to environmental-change. Ecology **76**:926-941.

Liu, S. and X. Meng. 1999. Modelling development time of *Myzus pesicae* (Hemiptera: Aphididae) at constant and natural temperatures. Bulletin of Entomological Research **89**:53-63.

Meehl, G. A. and C. Tebaldi. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science **305**:994-997.

Mondor, E. B. and B. D. Roitberg. 2000. Individual behaviour and population dynamics: lessons from aphid parasitoids. Entomologia Experimentalis et Applicata **97**:75-81.

Müller, C. B. and H. C. J. Godfray. 1999. Indirect interactions in aphid-parasitoid communities. Researches on Population Ecology **41**:93-106.

Muller, C. B., I. S. Williams, and J. Hardie. 2001. The role of nutrition, crowding and interspecific interactions in the development of winged aphids. Ecological Entomology **26**:330-340.

Noda, I. 1960. The Emergence of Winged Viviparous Female in Aphid V. Relation in the Development Between Wing buds and the Rest of the Body. The Ecological Society of Japan **10**:64-67.

Robinet, C. and A. Roques. 2010. Direct impacts of recent climate warming on insect populations. Integrative Zoology **5**:132-142.

Roitberg, B. D. and J. H. Myers. 1979. Behavioral and Physiological Adaptations of Pea Aphids (Homoptera Aphididae) to High Ground Temperatures and Predator Disturbance. Canadian Entomologist **111**:515-519.

Roux, O., C. Le Lann, J. J. M. van Alphen, and J. van Baaren. 2010. How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid Aphidius avenae (Hymenoptera: Aphidiidae)? Bulletin of Entomological Research **100**:543-549.

Satar, S., U. Kersting, and N. Uygun. 2008. Effect of temperature on population parameters of Aphis gossypii Glover and Myzus persicae (Sulzer) (Homoptera : Aphididae) on pepper. Journal of Plant Diseases and Protection **115**:69-74.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science **297**:1292-1296.

Sutherland, O. R. W. and T. E. Mittler. 1971. Influence of diet composition and crowding on wing production by the aphid Myzus persicae. Journal of Insect Physiology **17**:321-&.

Tahriri, S., A. A. Talebi, Y. Fathipour, and A. A. Zamani. 2007. Host stage preference, functional response and mutual interference of Aphidius matricariae (Hym.:

Braconidae : Aphidiinae) on Aphis fabae (Hom.: Aphididae). Entomological Science **10**:323-331.

Team, R. D. C. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Thomson, L. J., S. Macfadyen, and A. A. Hoffmann. 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control **52**:296-306.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Pages 2025-2034.

Villagra, C. A., C. C. Ramirez, and H. M. Niemeyer. 2002. Antipredator responses of aphids to parasitoids change as a function of aphid physiological state. Animal Behaviour **64**:677-683.

Wadley, F. M. 1923. Factors affecting the proportion of alate and apterous forms of aphids. Annals of the Entomological Society of America **16**:279-303.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Wann, M., D. Yen, and H. J. Gold. 1985. Evaluation and Calibration of 3 Models for Daily Cycle of Air-Temperature. Agricultural and Forest Meteorology **34**:121-128.

Zamani, A., A. Talebi, Y. Fathipour, and V. Baniameri. 2006. Temperature-dependent functional response of two aphid parasitoids, Aphidius colemani and Aphidius

matricariae (Hymenoptera : Aphidiidae), on the cotton aphid. Journal of Pest Science **79**:183-188.

Zamani, A. A., A. Talebi, Y. Fathipour, and V. Baniameri. 2007. Effect of temperature on life history of Aphidius colemani and Aphidius matricariae (Hymenoptera : Braconidae), two parasitoids of Aphis gossypii and Myzus persicae (Homoptera : Aphididae). Environmental Entomology **36**:263-271.

2.10 Appendix A: Model equations and functions

2.10.1 Model Equations

The subscript notation for the variables in the equations indicates the age class (1 = 1st instar, 5 = adult) and morphology *w* (1 = alate, 2 = apterous) respectively. The current aphid population, $A_{i,w}$, was the number of aphids of a given instar/morphology at time (*t*), and the probability of transition, *g(T),* determined how many hosts of a given instar transition to the next instar and how many remain in each time step based on temperature. Aphid reproduction, *r(T, Adensity),* was the number of aphids of a given morphology born during a time step and was dependent on temperature and overall aphid density. Aphid mortality, $d_{i,w}(T)$, was the combined mortality of the hosts due to chance, senescence, and temperature. The parasitoid's functional response, $n_{i,w}(T, A_{1,1}, P_2)$, was the number of aphids of the given age class/morphology removed during the time step by the parasitoids depending on the temperature, and the aphid and parasitoid populations at that time step. Once a host was been attacked, it was assumed that it was removed from the aphid population at that time, not when it was actually killed 5-7 days later. The aforementioned interactions and functions were included into the stage-structured transition matrix shown below.

$$a_{1,1} = \left[A_{1,1}\left(1 - g_{1,1\to 2,1}(T)\right)\right]\left(1 - d_{1,1}(T)\right) - n_{1,1}(T, A_{1,1}, P_2) \quad (2.1)$$

$$a_{2,1} = A_{1,1}\left(g_{1,1\to 2,1}(T)\right) \quad (2.2)$$

$$a_{2,2} = \left[A_{2,1}\left(1 - g_{2,1\to 3,1}(T)\right)\right]\left(1 - d_{2,1}(T)\right) - n_{2,1}(T, A_{2,1}, P_2) \quad (2.3)$$

$$a_{3,2} = A_{2,1}\left(g_{2,1\to 3,1}(T)\right) \quad (2.4)$$

$$a_{3,3} = \left[A_{3,1}\left(1 - g_{3,1\to 4,1}(T)\right)\right]\left(1 - d_{3,1}(T)\right) - n_{3,1}(T, A_{3,1}, P_2) \quad (2.5)$$

$$a_{4,3} = A_{3,1}\left(g_{1,1\to 2,1}(T)\right) \quad (2.6)$$

$$a_{4,4} = \left[A_{1,1}\left(1 - g_{1,1\to 2,1}(T)\right)\right]\left(1 - d_{4,1}(T)\right) - n_{4,1}(T, A_{4,1}, P_2) \quad (2.7)$$

$$a_{5,4} = A_{4,1}\left(g_{4,1\to 5,1}(T)\right) \quad (2.8)$$

$$a_{5,5} = A_{5,1}\left(1 - d_{5,2}(T)\right) - n_{5,1}(T, A_{5,1}, P_2) \quad (2.9)$$

$$a_{1,5} = r_{1,1}(T, Adensity) \quad (2.10)$$

$$a_{6,6} = \left[A_{6,2}\left(1 - g_{6,2\to 7,2}(T)\right)\right]\left(1 - d_{6,2}(T)\right) - n_{6,2}(T, A_{6,2}, P_2) \quad (2.11)$$

$$a_{7,6} = A_{6,2}\left(g_{6,2\to 7,2}(T)\right) \quad (2.12)$$

$$a_{7,7} = \left[A_{7,2}\left(1 - g_{7,2\to 8,2}(T)\right)\right]\left(1 - d_{7,2}(T)\right) - n_{7,2}(T, A_{7,2}, P_2) \quad (2.13)$$

$$a_{8,7} = A_{7,2}\left(g_{7,2\to 8,2}(T)\right) \quad (2.14)$$

$$a_{8,8} = \left[A_{8,2}\left(1 - g_{8,2\to 9,2}(T)\right)\right]\left(1 - d_{8,2}(T)\right) - n_{8,2}(T, A_{8,2}, P_2) \quad (2.15)$$

$$a_{9,8} = A_{8,2}\left(g_{8,2\to 9,2}(T)\right) \quad (2.16)$$

$$a_{9,9} = \left[A_{9,9}\left(1 - g_{9,2\to 10,2}(T)\right)\right]\left(1 - d_{9,2}(T)\right) - n_{9,2}(T, A_{9,2}, P_2) \quad (2.17)$$

$$a_{10,9} = A_{9,9}\left(g_{9,2\to 10,2}(T)\right) \quad (2.18)$$

$$a_{10,10} = A_{10,2}\left(1 - d_{10,2}(T)\right) - n_{10,2}(T, A_{10,2}, P_2) \quad (2.19)$$

$$a_{6,10} = r_{1,2}(T, Adensity) \quad (2.20)$$

The parasitoid population was described by eq. 3.1 through 3.4 where P_i was the number of parasitoids of that stage at a given time step *t*. The subscript notation i in the equations indicates the age class of the parasitoid (1 = juvenile, 2 = adult). The parasitoid's functional response, $n_{i,w}(T, A_{density}, P_2)$, determined the number of new parasitoids recruited during the time step through oviposition into all age classes of aphids. Parasitoid mortality, $d_i(T)$ was the mortality of the parasitoids due to random chance, senescence, and temperature and the probability of transition, $g(T)$, was the rate which determined how many juvenile parasitoids transitioned to adults in each time step based on temperature.

$$p_{11} = P_1\left(1 - d_1(T)\right)\left(1 - g_{1\to 2}(T)\right) \quad (3.1)$$

$$p_{21} = P_1\left(g_{1\to 2}(T)\right) \tag{3.2}$$

$$p_{22} = P_2\left(1 - d_2(T)\right) + \left(P_{1,t} \times g_{1\to 2}(T)\right) \tag{3.3}$$

$$p_{21} = \sum_{i=1}^{I=5}\sum_{w=1}^{W=2} n_{i,w}(T, Adensity, P_2) \tag{3.4}$$

2.10.2 Model Functions

Temperature and density-dependent aphid and parasitoid functions

Functions were used to describe the aphid and parasitoid development, reproduction, and mortality, since all of these processes are temperature and/or density dependent processes. Table 2-2 summarizes the functions and their purposes, table 2-3 lists the parameters, and which functions they were used in, and table 2-4 provides the actual parameter values used for the model.

Development rate g was measured as the probability of transitioning to the next age class. A similar function, parameterized appropriately for each organism, was used for the development of both the hosts and parasitoids.

$$g_{i\to i+1}(T)\begin{cases} \dfrac{\delta}{1+\varphi e^{-\sigma T_{(t)}}} & \mathrm{T}_{(t)} < T_{\max g}; \\ \dfrac{\delta}{1+e^{\omega\left(T_{(t)} - T_{\max g}\right)}} & \mathrm{T}_{(t)} \geq T_{\max g}; \end{cases} \tag{4}$$

In eq 4, T_{maxg} was the maximum development temperature for the organism (upper developmental threshold). The probability that the organism will transition to the next age class under ideal temperature conditions was δ. The position of the development curve in relation to temperature below T_{maxg} was determined by φ. The slope of the

development curve below T_{maxg} was determined by σ and ω determined the slope of the development curve above T_{maxg}.

Alate and apterous adult aphids can give rise to alate or apterous offspring. Aphid reproduction was modelled using two distinct functions (eq. 7.1 and 7.2). The fecundity per adult aphid m and proportion of alate and apterous offspring p_{al} were determined using equations 5 and 6.

$$m(T, Adensity)\begin{cases} \dfrac{\kappa\left(1-\left(\dfrac{1}{1+e^{-\rho(Adensity-D)}}\right)\right)}{1+\beta e^{-\lambda T_{(t)}}} & T_{(t)} < T_{\max m}; \\ \dfrac{\kappa\left(1-\left(\dfrac{1}{1+e^{-\rho(Adensity-D)}}\right)\right)}{1+e^{\xi\left(T_{(t)}-T_{\max m}\right)}} & T_{(t)} \geq T_{\max m}; \end{cases} \quad (5)$$

In eq. 5, (T_{maxm}) was the maximum temperature at which the adult aphids will produce offspring. The maximum number of offspring that could be produced per time step under ideal temperature conditions was κ. The position of the reproduction curve in relation to temperature below T_{maxm} was β. The slope of the reproduction curve below and above T_{maxm} was determined by λ and ξ respectively.

Density-dependent reproduction was added by modifying κ so that as the total number of aphids *Adensity* increased, the maximum reproductive rate decreased in a sigmoidal fashion. The slope of the density dependent reproductive curve was determined by ρ and the inflection point was D.

Adult alate and apterous aphids can give birth to both apterous and alate offspring, thus the proportion of alate offspring per time step was calculated for both the adult aphid populations using equation 6.

$$p_{al}(Adensity) = \frac{\alpha}{1 + \theta e^{-\tau Adensity_{(t)}}} \tag{6}$$

For eq. 6, α was the maximum proportion of alates that could be produced under ideal conditions for alate production. The position of the proportion alate curve in relation to *Adensity* was determined by θ. The slope of the proportion alate curve was determined by τ. The proportion of apterous offspring was 1 - $p_{al}(Adensity)$.

The overall combined number of alate and apterous offspring that were produced per time step was described by the two equations below.

$$r_{1,1}(T, Adensity) = \left(m(T, Adensity) \times p_{al}(Adensity) \times A_{5,1}\right) + \left(m(T, Adensity) \times p_{al}(Adensity) \times A_{5,2}\right) \tag{7.1}$$

$$r_{1,2}(T, Adensity) = \left(m(T, Adensity) \times \left(1 - p_{al}(Adensity)\right) \times A_{5,1}\right) + \left(m(T, Adensity) \times \left(1 - p_{al}(Adensity)\right) \times A_{5,2}\right) \tag{7.2}$$

The number of alate offspring produced by both alate and apterous parents was $r_{1,1}$, and the number of apterous offspring produced by both alate and apterous parents was $r_{1,2}$. Post-natal initiation of wing development was not included although that may be important for some aphids (Muller et al. 2001).

Parasitoid foraging speed (area searched per time step) was determined by the following function.

$$s(T)\begin{cases}\dfrac{v}{1+\eta e^{-\chi T_{(t)}}} & \mathrm{T}_{(t)} < T_{\max s}; \\ \dfrac{v}{1+e^{\iota\left(T_{(t)}-T\max s\right)}} & \mathrm{T}_{(t)} \geq T_{\max s}; \end{cases} \tag{8}$$

For eq. 8, T_{maxs} was the temperature at which the maximum parasitoid foraging speed occurs. The maximum proportion of area that an individual wasp can cover in one time step was v. The position of the foraging speed curve in relation to temperature below T_{maxs} was determined by η. The slope of the parasitoid foraging speed curve below T_{maxs} was determined by χ. The slope of the parasitoid foraging speed curve at when temperatures were above T_{maxs} was determined by ι.

The overall functional response of the parasitoids $n_{i,w}$ was calculated using equation 9. This function is an expansion of a type two functional response first introduced by (Holling 1959). It was modified to include multiple prey choices, preference for juvenile aphids, and differential acceptance and success rates based on aphid age class (see Mondor and Roitberg 2000).

$$n_{i,w} = \frac{A_{i,w}s(T)\mu_{i,w}(1-\varepsilon_{i,w})t_{timestep}}{1+\sum_{i=1}^{I=5}\sum_{w=1}^{W=2}\left(\begin{array}{c}(A_{i,w}s(T)\varepsilon_{i,w}th_{p(i,w)})+(A_{i,w}s(T)\mu_{i,w}(1-\varepsilon_{i,w})(th_{p(i,w)}+th_{a(i,w)}) \\ +(A_{i,w}s(T)(1-\mu_{i,w})(1-\varepsilon_{i,w})(th_{p(i,w)}+th_{a(i,w)})\end{array}\right)} \tag{9}$$

The probability of host rejection after assessing its suitability was ε. The probability that the attack will be successful after the host has been accepted μ. The time the wasps have to forage $t_{timestep}$, was equal to the length of the time step. The handling time of the parasitoid as it assesses the suitability of the host was *thp* and the additional handling time if the parasitoid oviposited into the host was *tha*. The total handling time for a successful oviposition was *thp* + *tha*.

Mortality due to temperature stress was a key factor when dealing with extreme environments. Equation 10 below describes the mortality rates of both the aphids and the parasitoids resulting from three sources: random chance, senescence, and temperature dependent.

$$d(T) = \zeta + \gamma + e^{(\psi(T - T_{\max d}))} \tag{10}$$

In eq. 10, ζ was the baseline mortality rate due to chance (excluding predation). The mortality in adult age classes due to senescence was γ. The temperature which mortality is 100% within a single time step was T_{maxd} and ψ was a shape parameter that influenced the slope of the temperature dependent mortality curve.

2.10.3 Tables

Table 2-4 Functions describing the temperature determination and population processes.

Function	Function description
T	Temperature determination
g	Aphid and parasitoid development
m	Per capita aphid reproduction
p_{al}	Proportion of alate offspring produced
r	Overall aphid reproduction
s	Parasitoid foraging speed (area covered)
n	Parasitoid functional response
d	Aphid and parasitoid mortality

Table 2-5 Parameters descriptions for temperature determination and population functions.

Symbol	Function	Parameter description
α	p_{al}	Maximum proportion of alates
β	*m*	Shifts position of reproduction curve in relation to temperature
γ	*d*	Mortality due to senescence in adult age classes
δ	*g*	Maximum probability of transition
ε	*n*	Probability of rejecting host
ζ	*d*	Background mortality
η	*s*	Shifts position of parasitoid foraging speed curve
θ	p_{al}	Shifts position of alate production curve in relation to *Adensity*
ι	*s*	Shifts slope of parasitoid foraging speed curve above T_{maxs}
κ	*m*	Maximum number of offspring that can be produced
λ	*m*	Shifts slope of reproduction curve below T_{maxm}
μ	*n*	Probability of successfully attacking a host
ν	*s*	Maximum area covered by foraging wasp
ξ	*m*	Shifts slope of reproduction curve above T_{maxm}
ρ	*m*	Shifts slope of density dependent reproduction curve
σ	*g*	Shifts slope of transition curve below T_{maxg}
τ	p_{al}	Shifts slope of alate production curve
φ	*g*	Shifts position of transition curve in relation to temperature
χ	*s*	Shifts slope of parasitoid foraging speed curve below T_{maxs}
ψ	*d*	Slope of temperature dependent mortality curve
ω	*g*	Shifts slope of transition curve above T_{maxg}
D	*b*	Inflection point on the density dependent reproduction curve
tha	*n*	Handling time of attack and oviposition after accepting a host
thp	*n*	Handling time for assessing prey suitability
Tmax	*T*	Maximum daily temperature
tmax	*T*	Time of maximum temperature
T_{maxd}	*d*	Temperature where there is 100% mortality due to temperature
T_{maxg}	*g*	Temperature where maximum probability of transition occurs
T_{maxm}	*m*	Temperature where maximum number of offspring produced
T_{maxs}	*s*	Temperature where maximum foraging rate occurs
Tmin	*T*	Minimum daily temperature
tmin	*T*	Time of minimum temperature
Tmin'	*T*	Minimum temperature of following day
tmin'	*T*	Time of minimum temperature the following day
$t_{timestep}$	*n*	Total number of seconds per time step

Table 2-6 Parameter values for aphid and parasitoid functions. (-) indicates parameter was not applicable for that age class.

Parameter	Value											
	Alate					Apterous					Parasitoid	
Age class	1st	2nd	3rd	4th	Adult	1st	2nd	3rd	4th	Adult	Juvenile	Adult
α	-	-	-	-	0.5	-	-	-	-	0.5	-	-
β	-	-	-	-	300.0	-	-	-	-	300.0	-	-
γ	-	-	-	-	0.003	-	-	-	-	0.003	-	0.0042
δ	0.027	0.027	0.027	0.027	0.027	0.027	0.027	0.027	0.027	0.027	0.0036	-
ε	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	-	-
ζ	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0032	0.0032
η	-	-	-	-	-	-	-	-	-	-	-	100.0
θ	-	-	-	-	20000.0	-	-	-	-	20000.0	-	-
ι	-	-	-	-	-	-	-	-	-	-		1.5
κ	-	-	-	-	0.17	-	-	-	-	0.33	-	-
λ	-	-	-	-	3.0	-	-	-	-	3.0	-	-
μ	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	-	-
ν	-	-	-	-	-	-	-	-	-	-		0.033
ξ	-	-	-	-	1.50	-	-	-	-	1.50	-	-
ρ	-	-	-	-	0.0	-	-	-	-	0.0	-	-
σ	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	-
τ	-	-	-	-	0.0007					0.0007	-	-
φ	150.0	150.0	150.0	150.0	150.0	150.0	150.0	150.0	150.0	150.0	200.0	-
χ	-	-	-	-	-	-	-	-	-	-	-	1.1
ψ	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4
ω	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	-
D	-	-	-	-	15000.0	-	-	-	-	15000.0	-	-
tha	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	-	-
thp	40.0	40.0	40.0	40.0	40.0	40.0	40.0	40.0	40.0	40.0	-	-
T_{maxd}	46.0	46.0	46.0	46.0	46.0	46.0	46.0	46.0	46.0	46.0	46.0	46.0
T_{maxa}	28.0	28.0	28.0	28.0	-	28.0	28.0	28.0	28.0	-	27.0	-
T_{maxm}	-	-	-	-	27.0	-	-	-	-	27.0	-	-
T_{maxs}	-	-	-	-	-	-	-	-	-	-	-	30.0

2.11 Connecting statement

In the preceding chapter, I modelled the effects of extreme and fluctuating temperatures on a theoretical aphid-parasitoid community. I showed that extreme, fluctuating temperatures had significant negative impacts on overall aphid-parasitoid community dynamics. Ambient temperature influences organisms in numerous ways. In the remaining chapters in my thesis I experimentally explore how extreme fluctuating temperatures impact specific interactions and mechanisms in an aphid-parasitoid community. Chapter 3 focuses on the effects of extreme fluctuating temperatures on indirect aphid-parasitoid interactions. Specifically, I examine how increasing extreme fluctuating temperatures impacts the strength of trait-mediated indirect interactions between foraging wasps and their aphid hosts.

3: The impacts of extreme and fluctuating temperatures on trait-mediated indirect aphid-parasitoid interactions

Jordan A. Bannerman, David R. Gillespie, Bernard D. Roitberg (2011) Ecological Entomology, **46**:490-498.

This work presented in this chapter was performed by and written by Jordan A. Bannerman under the guidance of Dr. Gillespie and Dr. Roitberg.

3.1 Abstract

1. Global climate change models predict an increase in the frequency and magnitude of extreme temperature events. These temperature events, heat waves for example, will impact a wide range of physiological and behavioural processes, particularly in ectotherms, and may therefore influence interactions between species.

2. Anti-predator responses may be more costly under more severe temperature regimes and therefore trait-mediated disturbance could lead to high mortality or reduced reproduction under extreme and fluctuating temperature regimes

3. We examined the impacts of extreme and fluctuating temperatures on trait-mediated indirect interactions in an aphid-parasitoid community.

4. In treatments that isolated the effects of trait-mediated disturbance from the effects of foraging parasitoids we found that an increase in both the amplitude and frequency of peak temperatures reduced aphid numbers and provided evidence that the cost of trait-mediated disturbance could increase under frequent periods of high temperature. Aphid dispersal also increased with more frequent periods of high temperature.

5. In treatments where female wasps were allowed to freely forage (direct + trait-mediated effects), there was no evidence that extreme and fluctuating temperatures influenced the wasp's foraging ability. Exposure to extreme fluctuating temperatures did not influence the offspring production of exposed wasps or the position of the mummies within the plots.

Keywords: Trait-mediated indirect effects, non-consumptive effects, trophic interactions, heat stress, *Aphidius matricariae*, *Myzus persicae,* climate change

3.2 Introduction

The warming associated with climate change is predicted to benefit agricultural pest insects due to an increase in the lower temperatures experienced which can increase overwinter survival and the ability to produce more generations in a year (Cannon 1998, Bale et al. 2002, Hazell et al. 2010). Current global climate change models also predict an increase in the frequency and severity of extreme temperature events (Meehl and Tebaldi 2004). Many temperate areas could therefore see an increase in episodic periods of extremely warm weather, i.e. heat waves. Heat waves are periods of one or more days, where the maximum temperature reached during the day is above seasonal norms (De Boeck et al. 2010). Heat waves are often accompanied by more sunshine and a larger vapour pressure deficit, factors that generally act as stressors. The amplitude (maximum and minimum temperatures) and the frequency of heat waves (how often and how regularly those hot days occur) are important variables that describe the strength of the heat wave. The implications of an increased frequency of severe high temperature events have not received much attention to date compared to research focused on the effects of low temperature limitations (Hance et al. 2007, Hazell et al. 2010).

Within communities, if temperatures unequally impact species growth and development in that community a phenological asynchrony may develop between the populations (Klapwijk et al. 2010). In addition to the impact of high temperatures on population-level processes, high temperatures may also influence direct and indirect processes occurring between trophic levels (Stenseth et al. 2002, Walther et al. 2002). One indirect process that might be influenced by extreme temperature in predator-prey or parasitoid-host communities is the non-consumptive effect caused by predator foraging

(i.e. trait-mediated indirect effect) (Werner and Peacor 2003). For example, under severe weather conditions, a host or prey may increase or decrease its defence responses, which would increase or decrease the strength of the interaction transmitted between the trophic levels.

Predators impact their prey both directly and indirectly through predation (Werner and Peacor 2003, for review). Indirect effects can impact prey mortality through modification of prey behaviour and morphology in the presence of predators; and these are generally referred to as trait-mediated indirect effects or non-consumptive effects (Werner and Peacor 2003, Abrams 2007). Recently there has been a focus on better understanding the impacts of these non-consumptive effects on community dynamics and function (e.g. Henry et al. 2010). An increase in extreme temperature events may exacerbate the impact of trait-mediated interactions within communities. Increases in temperature may alter the costs of defensive behaviours to hosts or prey, or may alter the value of the prey or host to the predator thereby changing the way in which they interact.

Behavioural and morphological modification of aphids in the presence of foraging parasitoids can be an important factor in the control of aphid populations (Kunert and Weisser 2003, Nelson et al. 2004). Aphids respond to predator or parasitoid-oviposition threats (hereafter referred to as foraging threats) in a number of ways. These include kicking, moving away, dropping from the plant, and alarm pheromone release which triggers a colony wide response (Roitberg et al. 1979). Aphid responses to foraging threats can be grouped into individual, patch, and global responses (Henry et al., 2010). Moreover, the range of responses can be grouped into direct and indirect impacts on the aphid population. Individuals that are consumed or parasitized directly reduce the aphid

population, but the remaining aphids that respond to the same threat may also be impacted though non-consumptive effects. Under stressful environmental conditions such as an increased temperature, the costs may increase relative to those under benign conditions, and therefore become more important for explaining the mortality and reduced reproductive output caused through direct and indirect interactions (Dill et al. 1990).

Our study system consisted of green peach aphids, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) feeding on sweet pepper, *Capsicum annuum* L. and of the parasitoid *Aphidius matricariae* (Haliday) (Hymenoptera: Braconidae). *Myzus persicae* is a major crop pest with a circumpolar distribution (Blackman and Eastop 1984). It causes damage to plants in several ways: it directly feeds on the phloem of the plant, reducing growth and vigour through developmental damage; it vectors a number of damaging plant viruses, and produces honeydew that blemishes and devalues the product (Brodsgaard and Albajes 1999). *Aphidius matricariae* is a parasitoid wasp of the green peach aphid (Giri et al. 1982). It is widely available as a commercial biological control agent for aphids, particularly green peach aphids (DRG pers obs). *Aphidius matricariae* is a large, fast moving, aggressive forager with a short handling time; once it locates a suitable host patch it will probe and oviposit into multiple hosts before moving on. When foraging, *A. matricariae* can be very disruptive, and causes patch-level antipredator responses in aphids (Henry et al. 2010).

In this study we examined the influence of frequency and severity of extreme temperature events on trait-mediated interactions between green peach aphids and *A. matricariae* by isolating and simulating the trait-mediated effects of foraging parasitoids

on aphid populations and comparing the resulting aphid populations to undisturbed aphid populations and aphid populations exposed to female parasitoids. We also examined the impacts of temperature stress on the parasitoids reproductive output.

3.3 Methods

3.3.1 Parasitoid production for behavioural assay

Several hundred *A. matricariae* were reared by exposing green peach aphids feeding on ten large excised pepper leaves to female parasitoids (Colony maintenance/rearing information provided in Appendix A). Eight adult female wasps and four adult male wasps were transferred into a 0.36 m^2 Bugdorm® containing the leaves and aphids and allowed to oviposit freely until they died. A 1L plastic jar with 5 3mm holes drilled out of the lid was filled with water and the petioles of the excised pepper leaves were inserted so that they were immersed in water. The leaves were replaced as needed (e.g. if the old leaf lost turgidity) until mummification occurred. Two days prior to the beginning of wasp emergence, the remaining living aphids were manually removed from the dried leaves to ensure newly-emerged wasps were naïve with respect to living aphids. Once the new generation of wasps began emerging, we moved the entire cage into a walk-in growth chamber (Conviron PWG56, with a CMP, Conviron Ltd. 590 Berry Street, Winnipeg Manitoba, Canada R3H 0R9).

3.3.2 Behavioural assay to determine trait-mediated responses

We performed behavioural assays to determine the patch-level, trait-mediated disturbance response of green peach aphids to *A. matricariae* attack under constant conditions, to establish the basic premise that trait-mediated responses, in the absence of

direct effects of the parasitoid, have the potential to lead to mortality or reduced reproductive rates in the aphid population. Assays were performed in a walk-in growth chamber at a constant 23°C temperature and 30-50% RH.

Three, aphid-covered, pepper plants from the colony were used as sources for plant and aphid material. All aphids and parasitoids were placed into the chamber at least 24 h prior to use, to acclimate them to the temperature and light conditions. Assays were run over three days with approximately one-third of the replicates completed on each day. Assays were conducted in 50 x 9mm Petri dishes (FALCON®, Franklin Lakes, NJ). A small piece of excised pepper leaf approximately 2 cm^2 that harboured between 8 and 12 green peach aphids with at least three different instars present was placed in the dish. The leaf pieces were approximately uniform in size, but the shapes differed as they were cut to include the appropriate number and composition of aphids from a leaf containing several hundred aphids. For ease of observation we limited the aphids to one side of the leaf by removing all aphids from the upper side of each patch.

Each assay began by allowing the wasp to move from a glass vial onto the lid of the Petri dish harbouring the aphids and then placing the lid over the bottom of the dish. For each trial, we recorded the time between the wasp's first contact with the leaf disc and its first sting (oviposition) attempt, and the total number of sting attempts over a three minute period, starting when the wasp first contacted the leaf disc. The disturbance of the patch of aphids resulting from the initial encounter (first sting attempt) was scored in four categories: no response, local response, patch response, or global response (Henry et al. 2010). If the aphid continued feeding after attack from the wasp it was considered a Non-Responder. If the attacked aphid ceased feeding and moved away from its current

location but none of the surrounding aphids responded, the outcome was classified as a Local Response. If more than one aphid that was not attacked directly ceased feeding and began to move after a wasp attack the outcome was classified as a Patch Level Response. Finally, if the attacked aphid released alarm pheromone the outcome was classified as a Global Response since all aphids in the surrounding area would receive that signal and react to it (Dixon 1958, Roitberg and Myers 1978). Global responses from subsequent stings were also noted.

3.3.3 Heat stress and trait-mediated interactions design

We investigated the effects of the frequency and amplitude of extreme temperature events, simulated trait-mediated indirect effects of foraging *A. matricariae*, and the effects of foraging parasitoids on aphid populations in growth chambers (Conviron E7 double, with controller models CMP 3244 and model CMP 4030, Controlled Environments Limited, 590 Berry Street, Winnipeg Manitoba, Canada R3H 0R9). Groups of five pepper seedlings in a tray, in a cage, were the experimental units. Details on these units are provided in the electronic supplement to this paper.

We used four temperature environments, each with a different combination of amplitude (maximum temperature) and frequency of peaks of temperature in a factorial design, in 7-day cycles (Figure 1). In the two low amplitude chambers (Figs 1a and 1b) the maximum temperature was 32°C, between 1230 and 1600, with a low temperature of 16.5°C between 2240 and 0600 the following morning. In the two high amplitude chambers, (Figs 1c and 1d), the maximum temperature was 40°C, with the peak temperature of 40°C at 1500. The low temperature during this cycle was 14.5°C, between 2300 and 0600 the following morning. In the low frequency chambers (Fig 1a and 1c),

these temperature programs were run twice in a 7 day cycle, on day 2 and 5. In the high-frequency treatment (Fig 1b and 1d), the chambers cycled through the temperature programs daily. The low frequency programs were preceded and followed by days with a constant 23°C, and the transitions were made at 2400. The temperatures were adjusted to provide a 24h average of 23°C, resulting in a compromise in the night temperatures, which were 2°C lower in the high amplitude chambers during the high amplitude cycle than in the low amplitude chambers. We refer to these treatments as Low amplitude-Low Frequency (LaLf), Low amplitude-High frequency (LaHf), High amplitude-Low frequency (HaLf) and High amplitude-High frequency (HaHf). Lighting was provided by GE Cool White tube lights, and the light intensity at plant canopy height was approximately 1200 lux. The day-night cycle was set at 16h day, 8 h night, with lights on at 06:00 and lights off at 22:00.

For each temperature treatment combination, we applied three disturbance regimes to assess the impacts of trait-mediated disturbance during the temperature stress caused by the extreme temperature events. In the DE + TME (Direct effects + Trait mediated effects) disturbance treatment, three female *A. matricariae* were introduced into experimental cages on each of day two and day five of the experiment. In the TME (Trait mediated effects only) treatment the disturbance of *A. matricariae* foraging on green peach aphids was simulated by physically prodding 15 feeding aphids in the abdomen, every day, using a fine-tipped toothpick, until they moved away from or dropped from the spot they were occupying. The TME treatment allowed us to simulate the trait-mediated effects without these being confounded with the direct effects that foraging wasps exert while foraging. The final disturbance treatment was the control treatment

where the aphids were allowed to develop undisturbed. Combined with the frequency and amplitude treatments, this produced a 2x2x3 full factorial experimental design. This experiment was performed six times, with three replicates of each of the twelve treatment combinations per run.

3.3.4 Heat stress and trait-mediated interactions experiment

One hundred green peach aphids of a standardized age range were added to the central plant in each plot of 5 pepper plants then the plots were placed into the experimental growth chambers (See Appendix A for details). The following day, three, mated, female *A. matricariae* were added to the DE + TME disturbance treatments and the TME treatment received its first round of disturbance. Plot/cage design and insect rearing details can be found in the online supplement. Control treatments received no disturbance over the course of the experiment and TME treatments were disturbed daily as described above. On day five of experiment, a second set of three parasitoids was introduced to the DE + TME treatment to ensure a constant presence of foraging wasps.

Eight days after the aphids were introduced, the plots were removed from the growth chambers and the aphid populations were counted. Aphids were counted on each plant, and the count from each plant was stratified into 5 categories: stem, cotyledons, first pair of leaves, second pair of leaves, and the crown (everything above the second pair of leaves). The plants in the DE + TME treatments were returned to their cages and were placed into a greenhouse under 16h light, 20°C to allow mummification to complete. The number and position of all parasitoid mummies was recorded seven days later.

3.3.5 Data analysis

All analyses were performed using JMP® 8.0.2 (SAS Institute 2009). The effect of disturbance, peak temperature, and the frequency of the temperature peaks on aphid population growth was analyzed with a Generalized Linear Model using a Poisson distribution and overdispersion tests (McCullough and Nelder 1989). Contrasts were used to test for differences between means. A similar analysis was performed to examine the effects of maximum temperature, and the frequency of the temperature peaks on the number of mummies produced. The data collected from the three pseudoreplicates (triplicate cages that received the same treatment combination) within each run were averaged to remove the pseudoreplication prior to analysis since the experimental unit was the growth chamber and the observational unit was the individual cages.

The spatial distribution of aphids within individual plants was also examined. Each plant was divided into five categories; stem, cotyledons, first pair of leaves, second pair of leaves, and the crown (all plant material above second set of full leaves). To examine the distribution of aphids and mummies on individual plants, the proportion of aphids and mummies found on each plant part was calculated. We used a MANOVA and contrasted the mean proportion of aphids on each plant part based on parasitoid disturbance, peak temperature amplitude, and peak temperature frequency as well as the two way interactions to determine if the distribution of aphids on each plant was affected by temperature treatments and parasitoid disturbance. To remove pseudoreplication the mean number of aphids on each plant part was averaged for the 15 plants in the three cages receiving the same treatment in each run of the experiment.

The distribution of aphids and mummies on central and perimeter plants, referred to as position within plot, was analysed using a MANCOVA and contrasted the mean proportion of aphids on each perimeter plant with the proportion of aphids on the central plant. Since the exterior plants were not considered to be independent, to analyze the data this way the proportion of aphids on each of the four exterior plants was summed and then averaged to generate the average number of aphids on one exterior plant. Peak temperature amplitude, peak temperature frequency, parasitoid disturbance treatment, and two way interactions were included in this analysis with aphid numbers in the cage (on all plants) included as a cofactor.

3.4 Results

3.4.1 Behavioural assay to determine trait-mediated responses

When *A. matricariae* individuals were introduced to the leaf patch containing the aphids the mean time to the first sting was 28 seconds (SE = 4.47 seconds). The mean number of sting attempts per minute once the patch of aphids was encountered by the parasitoid was 2.4 stings/minute (SE = 0.16). When the wasps were introduced into the Petri dish they generally took very little time to discover the patch and initiate foraging, although this time was not recorded because the wasps did not start at consistent locations. Of 54 wasps tested, five wasps did not attempt to oviposit into any aphids.

Of the 49 initial attacks, 60% (30) resulted in a local disturbance response by the attacked aphid, 26.5% (13) resulted in a patch level response and only two initial attacks resulted in global responses. In four initial attacks the aphid exhibited no response to the sting of the parasitoid. Out of 355 total sting attempts observed there were 9 global

responses which in almost every case led to a complete abandonment of the patch by all aphids.

3.4.2 Heat stress and trait-mediated interactions – Population effects

After 8 days we assessed the impact of extreme and fluctuating temperatures and trait-mediated disturbance on aphid numbers. Overall, the model examining the impact of amplitude, frequency, and disturbance on aphid numbers was highly significant (Generalized Linear Model, Poisson distribution, $\chi^2_9 = 928$, $P < 0.001$). The model was run with and without the three way interaction, and based on AIC scores, 117.9 without three way interaction and 121.1 with three way interaction, the model without the three way interaction was used (Akaike 1974, Johnson and Omland 2004). Aphid numbers were negatively influenced by the amplitude ($\chi^2_1 = 5.48$, $P = 0.020$) and frequency ($\chi^2_1 = 5.22$, $P = 0.022$) of the extreme temperature events, as well as by the disturbance treatment ($\chi^2_1 = 848$, $P < 0.0001$) (Figure 2). There were interactions between the amplitude and frequency of the temperature peaks ($\chi^2_1 = 4.57$, $P = 0.032$) and between the frequency of the temperature peak and the disturbance treatment ($\chi^2_2 = 12.33$, $P = 0.0021$). There may or may not be an interaction between the amplitude of the temperature peak and the disturbance treatment ($\chi^2_2 = 5.31$, $P = 0.07$). Contrasts indicated that the aphid numbers in the plots that received the TME treatment were lower than the control treatments receiving no disturbance ($\chi^2_1 = 5.35$, $P = 0.02$). In the absence of the direct effects of the foraging parasitoids, trait-mediated effects negatively influenced aphid numbers. In the DE + TME treatment there was no effect of amplitude ($\chi^2_1 = 0.03$, $P = 0.87$) or frequency ($\chi^2_1 = 1.03$, $P = 0.31$) on aphid numbers.

3.4.3 Heat stress and trait-mediated interactions –Spatial effects

When we examined the distribution of the aphids on individual plants classified by plant part, the highest numbers of aphids were found on the largest, lowest pair of fully expanded leaves on each plant. The crown and the smaller, higher set of full leaves held fewer aphids compared to the first pair of full leaves. Few aphids were found on the stem or the cotyledons. Our overall model indicated significant effects on the distribution of aphids (Wilks' Lambda, $F_{36,223} = 3.69$, P = < 0.001). In particular, the disturbance regime (Wilks' Lambda, $F_{8,118} = 6.56$, P = < 0.001) and the frequency of the temperature peaks (F test, $F_{4,59} = 14.13$, P = < 0.001) changed the distribution of the aphids. There appears to be an interaction between disturbance regime and the frequency of the temperature peaks (Wilks' Lambda, $F_{8,118} = 2.00$, P = 0.052). The DE + TME treatment reduced the proportion of aphids found on the crown and those aphids resettled on either set of true leaves or the cotyledons (Figure 3). The control and TME treatments did not appear to differ. An increase in the frequency of peak temperature led to more aphids on the first set of leaves and fewer on the cotyledons and crown.

When we examined the distribution of aphids within the plot of five plants there were generally more aphids on the central plants in each plot compared to the average number of aphids on the exterior plants (F test, $F_{10,61} = 3.27$, p = 0.002). A high (daily) frequency of temperature peaks led to a reduction of the proportion of aphids on the central plant and an increase in aphids spread between the four exterior plants (F test, $F_{1,61} = 11.3$, p = 0.0013) (Figure 4). Neither disturbance treatment (F test, $F_{2,61} = 2.34$, p = 0.10) nor the amplitude of the temperature peak (F test, $F_{1,61} = 0.06$, p = 0.81) influenced the spatial arrangement of aphids.

3.4.4 Heat stress and trait-mediated interactions –Parasitoid mummy formation

The number of parasitoid mummies in plots was not affected by the amplitude or frequency of the temperature peaks (Generalized Linear Model, Poisson distribution, $\chi^2_3 = 0.65$, $P = 0.88$). The number of mummies formed ranged from 55 to 535. The position of the mummies within plots was not influenced by the frequency or amplitude of the peak temperature (amplitude: $F_{1,69} = 0.60$, $P = 0.44$; frequency: $F_{1,69} = 0.79$, $P = 0.38$).

3.5 Discussion

Climate change can have important ecological consequences, influencing each trophic level, and interactions between trophic levels (Stenseth et al. 2002, Walther et al. 2002). Our work illustrates how temperature stress can negatively impact aphid populations, and how temperature stress may increase the costs of responding to trait-mediated disturbance. It also suggests that although the strength of indirect effects can be influenced by temperature they can easily be swamped in the presence of strong direct trophic interactions as likely happened in the DE + TME treatment. Experimental work that focuses only on changes in mean temperature may not be sufficient to characterize the important effects of changed temperature regimes. Variability and fluctuations in temperatures are also important factors,, particularly in communities that include ectotherms (Easterling et al. 2000, Walther et al. 2002).

In the presence of *A. matricariae*, a generally disruptive and aggressive parasitoid, each attack on a single aphid can influence the aphids around it approximately 40% of the time. Although the green peach aphids were not as reactive as some other species of aphids, such as the foxglove aphids, *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae) (Henry et al. 2010), the number of patch level responses indicates that under

stress the aphids responses could impact their fitness (Dill et al. 1990). Our TME treatment was designed to evoke these responses, and to isolate the impact of trait-mediated effects from the direct effects of parasitoids on the aphids. Although the TME treatment was designed to emulate the effect of foraging wasps we cannot be certain that our simulated attacks are an accurate reflection of parasitoid disturbance without oviposition. This is a limitation in this study system, since we were unable to use female wasps constrained so that they cannot actually oviposit into the aphids which would be equivalent to traditional manipulations of predators in trait-mediated indirect interaction studies (Werner and Peacor 2003).

In our main experiment, the interaction between the amplitude and frequency of the extreme temperature events indicated that these factors impact populations in an additive fashion. Increasing the frequency and the amplitude of extreme temperature events can lead to higher accumulations of developmental damage in aphids (Lamb 1961, Gullan and Cranston 2000), and the loss of beneficial endosymbionts (Ohtaka and Ishikawa 1991, Bensadia et al. 2006). We examined the effects of temperatures that were biologically relevant for both our species, with 32 °C approximately where green peach aphid development ceases, and some temperature dependent juvenile mortality occurs and parasitoids developing within their hosts would also be negatively impacted. At 40 °C significant temperature dependent mortality occurs for both species. Our results show that more variable extreme temperatures have a negative effect on aphid population growth irrespective of disturbance treatment.

Trait-mediated disturbances induced in the TME treatment were strong enough to reduce aphid populations, even over the short time scale of our experiment. In

conjunction with changes in the amplitude and frequency of temperature peaks increased thermal stress increased the impact of the trait-mediated effects on the aphid populations. Reduced aphid populations after continued disturbance may result from two processes. Aphid responses to physical disturbance may lead to mortality during the peak temperature periods, and second, aphid responses to physical disturbance may lead to reduced feeding rates and reduced rates of reproduction in the population.

The interaction between temperature frequency and disturbance indicated that the negative effects of indirect disturbance (TME treatment) may be amplified when the aphid population experiences frequent periods of high temperatures. This may be occurring in the DE + TME treatment as well but it is not clearly shown by our results since the direct effects of the parasitoid overshadow the weaker trait-mediated effects. This is a logical result since an increased frequency of temperatures that can harm the aphids and an increased occurrence of disturbed aphids in vulnerable positions (e.g. the soil surface after dropping from a plant) should increase the mortality that the aphids experience via desiccation and heat shock whether they are disturbed directly by female parasitoids or indirectly through an induced behavioural response (Dill et al. 1990). Regardless of the cause of the disturbance, the cost of the disturbance response to the aphid should increase with the frequency of stressful environmental conditions. Aphids are not always successful in returning to plants after disturbance, and desiccation and heat coma on the soil surface is an important source of mortality (Hodjat and Bishop 1978, Roitberg and Myers 1979, Dill et al. 1990).

Neither the frequency nor the amplitude of the temperature regimes influenced the aphid numbers in the DE + TME treatment. The DE + TME treatment had the largest

negative impact on aphid populations irrespective of temperature regime. The effects that three actively foraging parasitoids can exert on a small population of aphids may have overwhelmed the effects that the temperature regimes exerted on the aphid populations. Irrespective of aphid population size and temperature conditions, each group of female wasps produced a similar number of mummies after a week of foraging. This is counter to the results of Roux et al. (2010) who found exposure of *Aphidius avenae* (Haliday) (Hymenoptera: Braconidae) females to high temperature spikes had a negative influence of their fecundity. However, in our experiments, *A. matricariae* were exposed on whole plant communities with aphids, and had access to shelter, water and honeydew, whereas *A. avenae* were exposed in glass tubes without access to any resources (Roux et al. 2010). It is possible therefore that females in our experiments were able to withstand the high temperatures through behavioural adaptations.

The spatial distribution of aphids was influenced by disturbance treatment and the frequency of temperature peaks, at two spatial scales. At the individual plant level, aphids were displaced from the crown, and spread to lower parts of the plant (Figure 3). Green peach aphids prefer to feed on the crown or senescing older leaves, but the young, small plants that were used for this experiment did not feature older senescing leaves. If the plants were older, the distribution may have been distributed differently, possibly with an even higher proportion on the lower leaves. At the plot level, aphids were displaced from the central plant and dispersed to the exterior plants when exposed to an increased frequency of high temperature events (Figure 4). It appears that the aphids that were only physically disturbed (TME treatment) would freely re-establish on the plant, and even on the crown. The aphids exposed to the female parasitoids (DE + TME

treatment) either moved down the plant in response to the parasitoid or dropped from the plant and when they re-established they did so more often on a lower whorl of the plant.

At the population level, the frequency of temperature peaks not only reduced aphid numbers, but also increased the dispersal of the aphids away from where they were initially established. Increased movement of aphids increases the risk for the spread of aphid vectored plant viruses and disease (Roitberg and Myers 1978). From a biological control perspective, the reduction in aphid numbers is desirable, but the dispersal of aphids makes subsequent control more difficult (Henry et al. 2010).

Where the mummies formed was not affected by the temperature regime they developed in. The majority of the mummies formed on the undersides of the first set of true leaves or on the underside of the cotyledons. The mummies were also distributed throughout the plot, on all of the plants. In some aphid parasitoids there appears to be host modification which leads to patterns in where mummies are formed (Brodeur and McNeil 1989, 1992), but there is no evidence of this for *A. matricariae*, other than forming predominantly on the undersides of leaves out of direct light, which is where the majority of the aphids already occur.

The majority of temperature-based climate change research has focused the effects of increases in mean temperatures on organisms, but there is also research suggesting that increased temperature variance could also be important (Easterling et al. 2000, Walther et al. 2002). Increased temperature variance has been shown to impact species fitness and climatic stress resistance (Terblanche et al. 2010). Temporal desynchronization of phenology can also occur as a result of changes in variance (Harrington et al. 1999, Hulle et al. 2010). In some cases the effects of increased

temperature variance may actually counter the effects of an increase in mean temperature (Skirvin et al. 1997, Hulle et al. 2010). Our study has shown that differences in temperature variance can impact pest populations over a short time scale but we also saw that the effects of the temperature regimes appeared to be minimal for the parasitoids. Global warming will simultaneously affect all organisms but individual species responses to changes can result in complex cascading effects on aphid populations (Walther et al. 2002, Gilman et al. 2010, Robinet and Roques 2010)

Recently there has been an increased focus on identifying how climate change is influencing interactions between organisms (Suttle et al. 2007, Van der Putten et al. 2010). Species interactions are among the most important forces structuring ecological communities and are commonly climate-dependent (Gilman et al. 2010). We examined how indirect interactions between trophic levels were influenced by temperature variance and found that the strength of the effect of the indirect interactions differed based on the temperature regime and that trait-mediated disturbance can cause significant aphid mortality under stressful environmental conditions. The effects of trait-mediated disturbance are not apparent when there are direct effects also occurring as the latter masked the effects of the weaker indirect interactions in our study system.

It is difficult to generalize how interactions between trophic levels will be influenced by climate change since interactions are generally complex and few systems have been studied extensively (Hulle et al. 2010). There is theoretical and experimental evidence that warmer conditions may lead to better control of pests by parasitoids and predators (Skirvin et al. 1997, Bensadia et al. 2006). Heat shocks, not just changes in mean temperatures, have been shown to influence the susceptibility of insects to attack

from predators, parasitoids, and pathogens (Stacey and Fellowes 2002, Harmon et al. 2009, Hulle et al. 2010). Both an increased frequency of extreme temperature events and an increase in main temperature will influence trophic interactions and there is mounting evidence that increases in both average temperatures, and frequency of extreme temperature events will benefit the third trophic level more than the second trophic level in aphid-parasitoid communities.

3.6 Acknowledgements

This work would not have been possible without the help of P. Clarke, E. Quan, and A. Nasreen. Funding for this work was provided by an NSERC Strategic grant held by BDR and DRG.

3.7 Figures

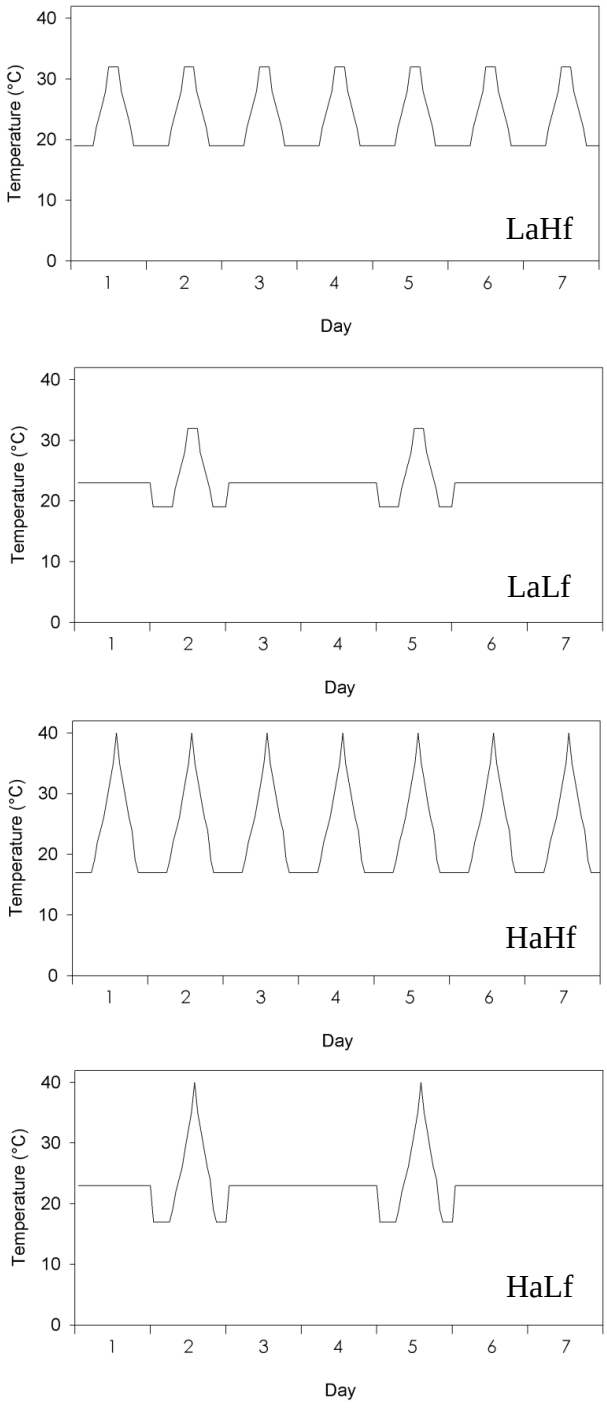

Figure 3-1 Heat wave regimes: 1a = 32 °C peaks daily, 1b = 32 °C peaks bi-weekly, 1c = 40 °C peaks daily, 1d = 40 °C peaks bi-weekly.

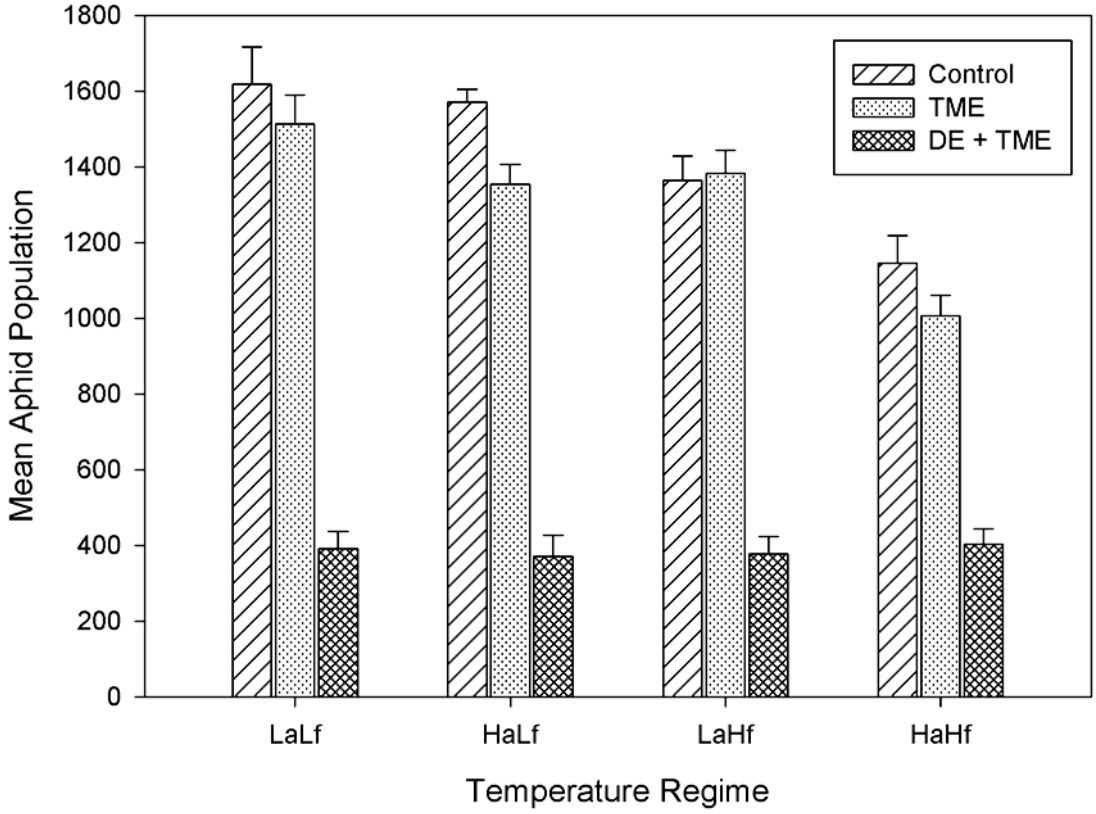

Figure 3-2 Mean ± SE (N=6) numbers of aphids 8 days after the initial release of 100 aphids on plots of 5 pepper plants under four different experimental heat wave regimes and three different trait-mediated disturbance regimes. LaLf = 32 °C peaks bi-weekly, LaHf = 32 °C peaks daily, HaLf = 40 °C peaks biweekly, HaHf = 40 °C peaks daily. Control = undisturbed aphids, TME = simulated female wasp foraging, DE + TME = foraging female wasps.

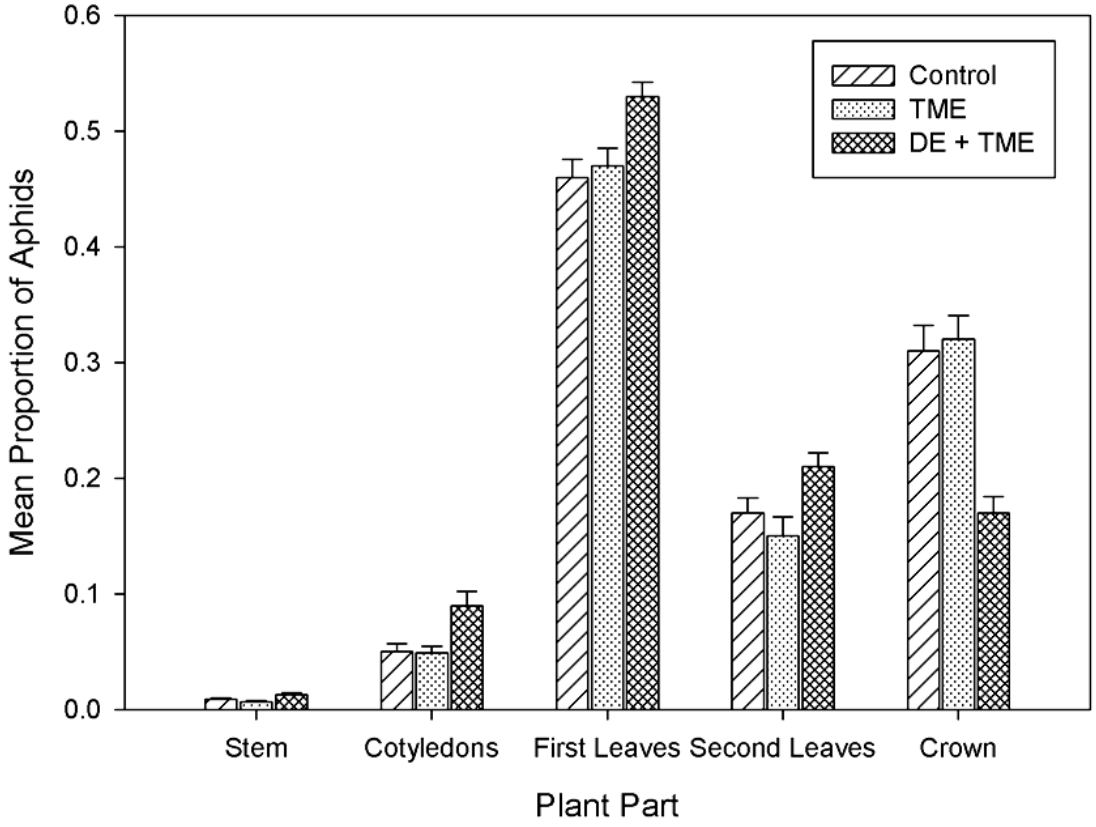

Figure 3-3 Mean ± SE (N=6) proportion of aphids found on each plant part irrespective of position within plot of 5 pepper plants under three different trait-mediated disturbance regimes. Control = undisturbed aphids, TME = simulated female wasp foraging, DE + TME = foraging female wasps.

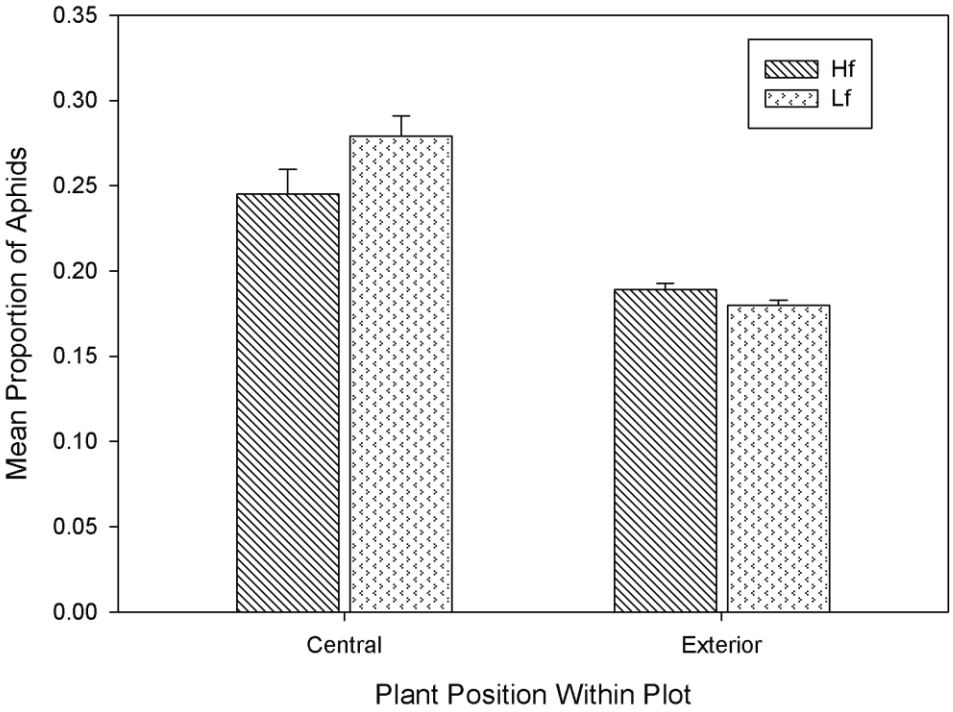

Figure 3-4 Mean ± SE (N=6) proportion of aphids found on central and exterior plants in plots of 5 pepper plants under four different experimental heat wave regimes. Exterior plant value is ¼ the proportion of aphids on all four exterior plants. Hf = temperature peaks daily, Lf = temperature peaks bi-weekly.

3.8 Literature cited

Abrams, P. A. 2007. Defining and measuring the impact of dynamic traits on interspecific interactions. Ecology **88**:2555-2562.

Akaike, H. 1974. New Look at Statistical-Model Identification. Ieee Transactions on Automatic Control **19**:716-723.

Angilletta, J., M.J. and A. E. Dunham. 2003. The temperature-size rule in ectotherms: Simple evolutionary explainations may not be generated. The American Naturalist **162**:332-342.

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology **27**:249-268.

Asin, L. and X. Pons. 2001. Effect of high temperature on the growth and reproduction of corn aphids (Homoptera: Aphididae) and implications for their population dynamics on the Northeastern Iberian Peninsula. Environmental Entomology **30**:1127-1134.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. Martijn Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. Hefin Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

Bensadia, F., S. Boudreault, J. F. Guay, D. Michaud, and C. Cloutier. 2006. Aphid clonal resistance to a parasitoid fails under heat stress. Journal of Insect Physiology **52**:146-157.

Bezemer, T. M., T. H. Jones, and K. J. Knight. 1998. Long-term effects of elevated CO_2 and temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. Oecologia **116**:128-135.

Bezemer, T. M., K. J. Knight, J. E. Newington, and T. H. Jones. 1999. How general are aphid responses to elevated CO_2? Annals of the Entomological Society of America **92**:724-730.

Birt, A., R. M. Feldman, D. M. Cairns, R. N. Coulson, M. Tchakerian, W. M. Xi, and J. M. Guldin. 2009. Stage-structured matrix models for organisms with non-geometric development times. Ecology **90**:57-68.

Blackman, R. L. and V. F. Eastop. 1984. Aphids on the world's crops, an identification guide. Wiley, New York.

Brodeur, J. and J. N. McNeil. 1989. Seasonal Microhabitat Selection by an Endoparasitoid through Adaptive Modification of Host Behavior. Science **244**:226-228.

Brodeur, J. and J. N. McNeil. 1992. Host Behavior-Modification by the Endoparasitoid Aphidius-Nigripes - a Strategy to Reduce Hyperparasitism. Ecological Entomology **17**:97-104.

Brodsgaard, H. F. and R. Albajes. 1999. Insect and mite pests. Pages 48-60 *in* R. Albajes, M. Lodovica Gullino, J. C. Van Lenteren, and Y. Elad, editors. Integrated pest and disease management in greenhouse crops. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Cannell, M. G. R. and J. H. M. Thornley. 1998. N-poor ecosystems may respond more to elevated [CO_2] than N-rich ones in the long term. A model analysis of grassland. Global Change Biology **4**:431-442.

Cannon, R. J. C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. Global Change Biology **4**:785-796.

Chown, S. L. and J. S. Terblanche. 2007. Physiological diversity in insects: Ecological and evolutionary contexts. Pages 50-152 Advances in Insect Physiology, Vol 33. Academic Press Ltd, London.

Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. Journal of Animal Ecology **67**:600-612.

Davis, J. A., E. B. Radcliffe, and R. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae). Physiological Ecology **35**:1461-1468.

De Boeck, H. J., F. E. Dreesen, I. A. Janssens, and I. Nijs. 2010. Climatic characteristics of heat waves and their simulation in plant experiments. Global Change Biology **16**:1992-2000.

De Wit, C. T. 1978. Simulation of Assimilation, Respiration and Transpiration of Crops. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Dill, L. M., A. H. G. Fraser, and B. D. Roitberg. 1990. The Economics of Escape Behavior in the Pea Aphid, Acrythosiphon-Pisum. Oecologia **83**:473-478.

Dixon, A. F. G. 1958. The escape responses shown by certain aphids to the presence of the coccinellis *Adalia decempuncta* (L.). Transactions of the Royal Entomological Society of London **110**:319-334.

Dixon, A. F. G. and S. D. Wratten. 1971. Laboratory studies on aggregation, size and fecundity in black bean aphid, *Aphis fabae* Scop. Bulletin of Entomological Research **6**:97-&.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate Extremes: Observations, Modeling, and Impacts. Science **289**:2068-2074.

Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO_2, ozone, and global climate change. Agriculture, Ecosystems and Environment **97**:1-20.

Gerling, D., B. D. Roitberg, and M. Mackauer. 1990. Instar-specific defense of the pea aphid, *Acyrthosiphon pisum*: Influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelmidae). Journal of Insect Behavior **3**:501-514.

Gillespie, D. R., A. Nasreen, C. Moffat, P. Clarke, and B. D. Roitberg. 2011. Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids and two parasitoid species. Oikos ***In Press.***

Gillespie, D. R., D. J. M. Quiring, R. G. Foottit, S. P. Foster, and S. Acheampong. 2009. Implications of phenotypic variation of Myzus persicae (Hemiptera: Aphididae) for biological control on greenhouse pepper plants. Journal of Applied Entomology **133**:505-511.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution **25**:325-331.

Giri, M. K., B. C. Pass, K. V. Yeargan, and J. C. Parr. 1982. Behaviour, net reproduction, longevity, and mummy-stage survival of Aphidius matricariae [Hym. Aphididae]. Entomophaga **27**:147-153.

Gullan, P. J. and P. S. Cranston. 2000. The insects: an outline of entomology. Blackwell Publishing, Malde, MA.

Hance, T., J. van Baaren, P. Vernin, and G. Boivin. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology **52**:107-126.

Harmon, J. P., N. A. Moran, and A. R. Ives. 2009. Species Response to Environmental Change: Impacts of Food Web Interactions and Evolution. Science **323**:1347-1350.

Harrington, R., R. A. Flemming, and I. P. Woiwod. 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? Agricultural and Forest Entomology **3**:233-240.

Harrington, R., I. Woiwod, and T. Sparks. 1999. Climate change and trophic interactions. Trends in Ecology & Evolution **14**:146-150.

Hazell, S. P., B. P. Neve, C. Groutides, A. E. Douglas, T. M. Blackburn, and J. S. Bale. 2010. Hyperthermic aphids: Insights into behaviour and mortality. Journal of Insect Physiology **56**:123-131.

Henry, L. M., J. A. Bannerman, D. R. Gillespie, and B. D. Roitberg. 2010. Predator identity and the nature and strength of food web interactions Journal of Animal Ecology **79**:1164-1171

Hodjat, S. H. and G. W. Bishop. 1978. Effects of Crowding on Clonal Cultures of Myzus-Persicae (Sulz). Entomologia Experimentalis et Applicata **24**:178-184.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist **91**:385–398.

Huey, R. B. and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. TRENDS in Ecology and Evolution **4**:131-135.

Hulle, M., A. Coeur d'Acier, S. Bankhead-Dronnet, and R. Harrington. 2010. Aphids in the face of global changes. Comptes Rendus Biologies **333**:497-503.

Ives, A. R. 1995. Predicting the response of populations to environmental-change. Ecology **76**:926-941.

Johnson, J. B. and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution **19**:101-108.

Karl, T. R. and K. E. Trenbeth. 2003. Modern global climate change. Science **302**:1719-1723.

Klapwijk, M. J., B. C. Grobler, K. Ward, D. Wheeler, and O. T. Lewis. 2010. Influence of experimental warming and shading on host-parasitoid synchrony. Global Change Biology **16**:102-112.

Kunert, G. and W. W. Weisser. 2003. The interplay between density- and trait-mediated effects in predator-prey interactions: a case study in aphid wing polymorphism. Oecologia **135**:304-312.

Lamb, K. P. 1961. Some Effects of Fluctuating Temperatures on Metabolism, Development, and Rate of Population-Growth in Cabbage Aphid, Brevicoryne Brassicae. Ecology **42**:740-745.

Liu, S. and X. Meng. 1999. Modelling development time of *Myzus pesicae* (Hemiptera: Aphididae) at constant and natural temperatures. Bulletin of Entomological Research **89**:53-63.

McCullough, P. and J. A. Nelder. 1989. Generalized linear models. Monographs on statistics and applied probability 37. Chapman & Hall, New York.

Meehl, G. A. and C. Tebaldi. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science **305**:994-997.

Mondor, E. B. and B. D. Roitberg. 2000. Individual behaviour and population dynamics: lessons from aphid parasitoids. Entomologia Experimentalis et Applicata **97**:75-81.

Müller, C. B. and H. C. J. Godfray. 1999. Indirect interactions in aphid-parasitoid communities. Researches on Population Ecology **41**:93-106.

Muller, C. B., I. S. Williams, and J. Hardie. 2001. The role of nutrition, crowding and interspecific interactions in the development of winged aphids. Ecological Entomology **26**:330-340.

Nelson, E. H., C. E. Matthews, and J. A. Rosenheim. 2004. Predators reduce prey population growth by inducing changes in prey behavior. Ecology **85**:1853-1858.

Noda, I. 1960. The Emergence of Winged Viviparous Female in Aphid V. Relation in the Development Between Wing buds and the Rest of the Body. The Ecological Society of Japan **10**:64-67.

Ohtaka, C. and H. Ishikawa. 1991. Effects of heat treatment on the symbiotic system of an aphid mycetocyte. Symbiosis **11**:19-30.

Robinet, C. and A. Roques. 2010. Direct impacts of recent climate warming on insect populations. Integrative Zoology **5**:132-142.

Roitberg, B. D. and J. H. Myers. 1978. Effect of Adult Coccinellidae on the Spread of a Plant-Virus by an Aphid. Journal of Applied Ecology **15**:775-779.

Roitberg, B. D. and J. H. Myers. 1979. Behavioral and Physiological Adaptations of Pea Aphids (Homoptera Aphididae) to High Ground Temperatures and Predator Disturbance. Canadian Entomologist **111**:515-519.

Roitberg, B. D., J. H. Myers, and B. D. Frazer. 1979. Influence of Predators on the Movement of Apterous Pea Aphids between Plants. Journal of Animal Ecology **48**:111-122.

Roux, O., C. Le Lann, J. J. M. van Alphen, and J. van Baaren. 2010. How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid Aphidius avenae (Hymenoptera: Aphidiidae)? Bulletin of Entomological Research **100**:543-549.

SAS-Institute. 2009. JMP 8.0.2. SAS-Institute, Cary NC.

Satar, S., U. Kersting, and N. Uygun. 2008. Effect of temperature on population parameters of Aphis gossypii Glover and Myzus persicae (Sulzer) (Homoptera : Aphididae) on pepper. Journal of Plant Diseases and Protection **115**:69-74.

Sibly, R. M. and D. Atkinson. 1994. How rearing temperature affects optimal adult size in ectotherms. Functional Ecology **8**:486-493.

Skirvin, D. J., J. N. Perry, and R. Harrington. 1997. The effect of climate change on an aphid-coccinellid interaction. Global Change Biology **3**:1-11.

Stacey, D. A. and M. D. E. Fellowes. 2002. Influence of temperature on pea aphid Acyrthosiphon pisum (Hemiptera : Aphididae) resistance to natural enemy attack. Bulletin of Entomological Research **92**:351-357.

Stary, P. 1970. Biology of Aphid Parasites, The Hague.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science **297**:1292-1296.

Sutherland, O. R. W. and T. E. Mittler. 1971. Influence of diet composition and crowding on wing production by the aphid Myzus persicae. Journal of Insect Physiology **17**:321-&.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science **315**:640-642.

Tahriri, S., A. A. Talebi, Y. Fathipour, and A. A. Zamani. 2007. Host stage preference, functional response and mutual interference of Aphidius matricariae (Hym.: Braconidae : Aphidiinae) on Aphis fabae (Hom.: Aphididae). Entomological Science **10**:323-331.

Team, R. D. C. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Terblanche, J. S., N. C., and E. Kleynhans. 2010. Thermal variability alters climatic stress resistance and plastic responses in a globally invasive pest, the Mediterranean fruit fly (*Ceratitis capitata*). Entomologia Experimentalis et Applicata **137**:304-315.

Thomson, L. J., S. Macfadyen, and A. A. Hoffmann. 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control **52**:296-306.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Pages 2025-2034.

Villagra, C. A., C. C. Ramirez, and H. M. Niemeyer. 2002. Antipredator responses of aphids to parasitoids change as a function of aphid physiological state. Animal Behaviour **64**:677-683.

Vitousek, P. M. 1994. Beyond global warming - ecology and global change. Ecology **75**:1861-1876.

Wadley, F. M. 1923. Factors affecting the proportion of alate and apterous forms of aphids. Annals of the Entomological Society of America **16**:279-303.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Wann, M., D. Yen, and H. J. Gold. 1985. Evaluation and Calibration of 3 Models for Daily Cycle of Air-Temperature. Agricultural and Forest Meteorology **34**:121-128.

Werner, E. E. and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology **84**:1083-1100.

Zamani, A., A. Talebi, Y. Fathipour, and V. Baniameri. 2006. Temperature-dependent functional response of two aphid parasitoids, Aphidius colemani and Aphidius

matricariae (Hymenoptera : Aphidiidae), on the cotton aphid. Journal of Pest Science **79**:183-188.

Zamani, A. A., A. Talebi, Y. Fathipour, and V. Baniameri. 2007. Effect of temperature on life history of Aphidius colemani and Aphidius matricariae (Hymenoptera : Braconidae), two parasitoids of Aphis gossypii and Myzus persicae (Homoptera : Aphididae). Environmental Entomology **36**:263-271.

3.9 Appendix A

3.9.1 Aphid and parasitoid colony maintenance

Green peach aphid colonies originated from collections from commercial greenhouses in Abbotsford, British Columbia Canada by DRG. From the original collections, DRG isolated the light green morph for further propagation (Gillespie et al. 2009). All green peach aphid colonies were maintained continuously on 6-8 week old sweet pepper plants in 0.36 m^2Bugdorms® (BioQuip Products, Rancho Dominguez, CA) at the Pacific Agri-Food Research Centre, Agassiz British Columbia. Colonies were maintained under GE Cool White tube lights at 21°C on a 16h day 8h night cycle at 40-60% relative humidity. Two of the plants were replaced with new, clean pepper plants to keep the populations in check on a weekly basis. The two aphid-infested plants that were from the aphid colony cage were moved each week into a cage containing adult *A. matricariae* to provide hosts for parasitoid reproduction. *A. matricariae* were reared under the same light and temperature conditions in Bugdorms®. All pepper plants were propagated in a soilless mixture containing 65% peat, 35% perlite, and were watered with a 1% solution of 20-20-20 fertilizer. These colonies were the source for all insects used in the experiments described here.

3.9.2 Plant production for heat stress and trait-mediated interactions experiment

Experimental plots of sweet pepper were constructed by planting 5 small pepper plants (cotyledons and 1 set of true leaves present at time of transfer) in an X pattern in a 3 cell by 3 cell plastic plant tray. The individual cells were 5.5 cm square by 7 cm deep, and the entire tray was 18 cm square. The centre cell, and the four corner cells received

plants, and the remaining four cells contained only soil. When the pepper plants were three weeks old, each tray was enclosed by covering a frame constructed of wire with Agryl P17 spun-bond row cover (BBA Fiberweb, London, UK). This cage was placed into a 20 cm diameter plant saucer so that water could be added from the bottom without disturbing the plants and insects. The top of each cage was closed with a clip which could be removed for access so that the trait-mediated cue could be easily applied without additional mechanical disturbance imparted on the entire plot.

3.9.3 Aphid production for heat stress and trait-mediated interactions experiment

Green peach aphids were produced by placing 180 apterous adult green peach aphids onto excised pepper leaves in leaf cups. The aphids were allowed to produce nymphs for three days. Leaf cups were constructed by filling the bottom of a Styrofoam cup (Dixie SM8, Georgia Pacific Ltd, Atlanta GA, USA) with approximately 30 ml of water, covering the water with a Solo cup (P200, Solo Cup Company, Urbana IL, USA) with a 3mm hole in it along one edge. An excised 6-8 week old pepper leaf was placed into the cup with the petiole through the hole so it was immersed in water. The cup was then capped with a Kimwipe® (Kimberly-Clark Inc. Dallas TX, USA) held in place by an elastic band. After three days, the adults were transferred to a second set of cups where they were left for two days. After two days they were transferred to a third set of cups and allowed to produce nymphs for three more days. This method produced three distinct age classes of aphids. When the experiment was initiated, 33±1 aphids from each age class were transferred onto a small, excised pepper leaf and allowed to settle before the leaf was transferred onto the centre plant in experimental plots. As the small leaf

wilted, the aphids moved onto the central plant thereby minimizing initial disturbance of the aphids.

3.9.4 Parasitoid production for heat stress and trait-mediated interactions experiment

A. matricariae were reared by introducing 8 female and 4 male wasps into a Bugdorm®, as described in the Parasitoid production for behavioural assay section, 13 days prior to the start of the experiment. A second introduction of *A. matricariae* was required three days after the initial introduction, so a second *A. matricariae* cage was produced using the same method, three days after the first cage was started.

3.10 Connecting statement

In this chapter, I found that extreme fluctuating temperatures reduced the effect of *A. matricariae* on aphid populations. Extreme fluctuating temperatures did not influence the number of progeny *A. matricariae* was able to produce however. This result fails to provide a complete picture of how extreme fluctuating temperature regimes influence the life history and performance of the parasitoids. Chapter 4 explores the effects of temperatures on the life history of *A. matricariae* developing under extreme fluctuating environments. I assessed adult life history traits under common conditions after exposing larval parasitoids to a range of extreme and fluctuating temperature throughout development.

4: Impact of extreme and fluctuating temperatures during larval development on the life history traits of *Aphidius matricariae*

Jordan A. Bannerman, David R. Gillespie, Bernard D. Roitberg.

All research presented in this chapter was performed by J. Bannerman

4.1 Abstract

Shifts in temperature regimes that may occur through global climate change can have major ecological implications. The fitness, physiology, and behaviour of insects is determined by ambient temperature. It is important to determine how climate change will impact keystone organisms within communities, such as parasitoids. I examined the life history traits of *Aphidius matricariae* wasps that developed under five extreme and fluctuating temperature regimes. I assessed the development time, lifetime reproductive output, longevity and then calculated the population-level reproductive rate of wasps reared under each of the temperature regimes. Development was delayed by an increase in the frequency of extreme temperature pulses, but there were no clear effects of temperature regimes on wasp longevity or lifetime fecundity.

Keywords: heat wave; *Aphidius matricariae*; *Myzus persicae*; climate change; heat shock; life history.

4.2 Introduction

Shifts in temperature regimes that may occur through global climate change can have major ecological implications (Stenseth et al. 2002, Walther et al. 2002). To date, much of the focus of climate change research has been on the effects of a reduction in lower temperature limitations, an increase in the number of generations produced in a year and increased overwinter survival, which is predicted to benefit many pest species (Cannon 1998, Bale et al. 2002, Hance et al. 2007, Hazell et al. 2010) . However, climate change models also predict an increase in the frequency and amplitude of extreme temperature events, particularly hot events during the summer months in temperate regions (Easterling et al. 2000, Meehl and Tebaldi 2004).

Ambient temperature influences the physiology, development, behaviour and life history of insects, since their body temperature depends on ambient temperature (Roux et al. 2010). Insects and other organisms have thermal ranges to which their physiological functions are optimized (Angilletta et al. 2002, Chown and Terblanche 2007). When temperatures exceed these optimal thermal ranges the insects can become stressed, resulting in behavioural and physiological changes that may influence their fitness (Angilletta et al. 2002, Chown and Terblanche 2007).

In addition, organisms that have a restricted capacity for movement, such as immature parasitoids, are generally unable to modify their environmental conditions, which further links their life history to ambient environmental conditions (Hance et al. 2007). Thus, juvenile koinobiont parasitoids must deal with the thermal stress imposed on their host because to survive to maturity the parasitoid's host must also survive (Hance et al. 2007). Given the vulnerability of the developing parasitoids to thermal stress,

exposure to extreme and fluctuating temperatures in the immature stages of the organisms' development may play a key role in determining the subsequent life history and fitness of the adult insects (Roux et al. 2010). Roux et al. (2010) subjected newly emerged adult *Aphidius* wasps to short heat shocks and found that these shocks had a serious impact on the subsequent fitness of the wasps. Similar effects may occur if juvenile wasps were subjected to heat shocks or periodic heat stress.

Aphidius matricariae (Haliday) (Hymenoptera: Braconidae) is a parasitoid which attacks the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) (Giri et al. 1982). It is commercially available as a commercial biological control agent for green peach aphids in agricultural settings and therefore both ecologically and economically important (DRG pers comm.). It is able to successfully complete development at temperatures up to 30 °C (Giri et al. 1982). Juvenile development takes approximately 12 days at 21 °C and the maximum development rate occurs at 25 °C when *M. persicae* is the host (Zamani et al. 2007). Even short periods (0.5 hours) of extreme temperatures during development have been found to delay *A. matricariae* development substantially, which may adversely impact the abilities of the wasps to effectively control aphid populations (Hodson and Gillespie 2010 , Unpublished data).

We subjected parasitized green peach aphids containing developing *A. matricariae* to five extreme and fluctuating temperature regimes throughout development from the egg to the emerged adult and then quantified the fitness and life history traits of the emergent female wasps under common conditions. We expected to see a decrease in lifetime fecundity as environmental conditions increased in severity and expected to see

differences in adult longevity although it was not clear if it would increase or decrease longevity based on previous studies on a related *Aphidius* sp. (Roux et al. 2010).

4.3 Methods

4.3.1 Aphid and parasitoid colony maintenance

Green peach aphid colonies originated from field collections from commercial greenhouses in Abbotsford, British Columbia Canada by DRG. From the original field collections, DRG isolated a light green morph for further propagation (Gillespie et al. 2009). Green peach aphid colonies were maintained in 1 m^2cages (Bugdorms®, BioQuip Products, Rancho Dominguez, CA) containing 4, 6-8 week old sweet pepper, *Capsicum annuum L.*, plants at the Pacific Agri-Food Research Centre, Agassiz British Columbia. Colonies were maintained under GE Cool White tube lights at 21°C 40-60% relative humidity. Two of the plants in each colony cage were replaced weekly with new, uninfested pepper plants to keep populations at manageable levels. Two aphid-infested plants were moved into a cage containing adult *A. matricariae* weekly to provide hosts for parasitoid reproduction. The *A. matricariae* were reared under the same light and temperature conditions as the green peach aphids in 1 m^2cages. All pepper plants were propagated in a soilless mixture containing 65% peat, 35% perlite, and were watered with a 1% solution of 20-20-20 fertilizer at every watering. These colonies were the source of all insects used for the experiments described below.

4.3.2 Parasitoid life history

We allowed wasps to oviposit into aphids, and then subjected those parasitized aphids to one of five temperature regimes until development was complete. We then assessed the daily oviposition of the wasps until death.

4.3.3 Temperature regimes

We used five temperature regimes, each with a different combination of amplitude (maximum peak temperature) and frequency of peaks of temperature, in 7 day cycles (Figure 1). Figure 1 does not show the 5th temperature environment, which was a constant 23°C. In the two low amplitude chambers (Figs 1a and 1b) the maximum temperature was 32°C, between 1230 and 1600, with a low temperature of 16.5°C between 2240 and 0600 the following morning. In the two high amplitude chambers, (Figs 1c and 1d), the maximum temperature was 40°C, with the peak temperature of 40°C at 1500. The low temperature during this cycle was 14.5°C, between 2300 and 0600 the following morning. In the low frequency chambers (Fig 1a and 1c), these temperature programs were run twice in a 7 day cycle, on day 2 and 5. In the high-frequency treatment (Fig 1b and 1d), the chambers cycled through the temperature programs daily. The low frequency programs were preceded and followed by days with a constant 23°C, and the transitions were made at 2400. The temperatures were adjusted to provide a 24h average of 23°C, resulting in a compromise in the night temperatures, which were 2°C lower in the high amplitude chambers during the high amplitude cycle than in the low amplitude chambers. Lighting was provided by GE Cool White tube lights, and the light

intensity at plant canopy height was approximately 1200 lux. The day-night cycle was set at 16h day, 8 h night, with lights on at 06:00 and lights off at 22:00.

We refer to these treatments as Low amplitude-Low frequency (LaLf), Low amplitude-High frequency (LaHf), High amplitude-Low frequency (HaLf), High amplitude-High frequency (HaHf) and Constant (Const).

4.3.4 Production of aphids for experiment

Twenty-five adult green peach aphids were placed onto each of twenty-five, five-week-old pepper plants in plant cages. The adult aphids were removed three days later, leaving only the offspring produced during the preceding three days. The plants were then potted individually into 10 cm square pots in soilless media and were covered with transparent , 24.2 X 48.4 cm, microperforated cellophane bags (Chantler Packaging, 880 Lakeshore Drive, Mississauga Ontario Canada L5E 1E1), held in place with an elastic band on along the top edge of the pot.

4.3.5 Production of parasitoids for experiment

A. matricariae adults were produced by placing 15 excised pepper leaves, with their petioles through the lid of a 1 L plastic container filled with water, into a 0.36 m^2cages. Approximately 1000 green peach aphids were then distributed among the excised leaves, then five female and three male *A. matricariae* were added to the cage. Twelve days later, once the wasps began emerging, they were aspirated in groups of approximately 50, into capped 150 ml plastic cup containing a water wick and a supply of 5% sugar solution. The wasps remained in the container for 24h prior to use for the experiment. It was assumed that all of the female wasps would have mated since the

males vigorously seek out mates and the males generally outnumbered the females in these containers; and therefore there was no shortage of mating opportunities. The day following the removal of the adult aphids from the plant cage I placed a single mated *A. matricariae* female into the plant cage and allowed her to oviposit for three days on the aphids before she too was removed from the cage, producing a cohort of one to three day old immature wasps. All *A. matricariae* females that were used were between 24h and 36h old.

4.3.6 *Temperature exposure*

After I removed the wasps from the plant cages, five cages were placed into each of the five temperature regimes. The constant treatment was maintained in the temperature controlled growth room, while the other 4 treatments were maintained in growth chambers. All plants were kept under these conditions until wasp emergence, which began between 12 and 15 days depending on temperature treatment. We then moved each individual plant into separate cages in the greenhouse as wasps began emerging. Again, the wasps were aspirated in groups of approximately 50 into capped 150 ml plastic cup containing a water wick and a supply of 5% sugar solution and the wasps remained in the container for 24h prior to use.

4.3.7 Wasp fitness assay

From each cup we then collected three female wasps (75 in total) and used them to assess lifetime fecundity and longevity. Each wasp that was tested was transferred into a fresh leaf cup containing approximately 200 first and second instar aphids on an excised pepper leaf with its petiole immersed in water. Surviving wasps were transferred into a

fresh leaf cup every day (stopped after 9 days). Leaf cups were produced by placing fifteen adult aphids onto a single excised pepper leaf for three days prior to the day they were used. The adult aphids were removed immediately before the wasp was transferred into the cup. Leaf cups were maintained in a 23 °C growth room until emergence of the next generation of wasps. We counted the mummies in each cup nine days after oviposition and we collected all of the wasps that had emerged by thirteen days after oviposition and preserved them in 95% ethanol. This experiment was carried out once.

The number of offspring produced each day, the total offspring produced, the sex ratio of those offspring, and the longevity of each wasp was recorded. In order to illustrate the relationship between wasp longevity and offspring production a regression was performed. I calculated the population level reproductive rate (Euler's exact r) of the wasps from each temperature regime using the formulae found in Begon et al. 1996.

Since there was no true replication in this experiment the majority of the data are presented as observational data and not further analysed. Instead the data are used to highlight and suggest how heat wave regimes appear to be influencing the life history and performance of female *A. matricariae* wasps.

4.4 Results

The temperature regime that the juvenile wasps developed under influenced their development time (Table 1). Wasps reared in the Constant, LaLf, and HaLf regimes began emerging from their mummies after 12 days. Individuals reared under the LaHf regime began emerging after 13 days, and the wasps reared under the HaHf regime began emerging after 15 days. Daily periods of extreme temperature appeared to delay the

development of the wasps and the maximum temperature of that peak temperature also appeared to be important.

The mean number of offspring that the wasps produced was calculated for each temperature regime and summarized in Table 1. The maximum number of mummies produced by an individual wasp was 494. The variation in numbers of mummies produced between individuals was very high regardless of the heat wave regime in which they were reared. A large source of variation in offspring production can be attributed to the variation in longevity of the wasps. Regardless of temperature regime, there was a clear positive relationship between wasp longevity and number of offspring that they produced (Regression, F ratio = 237, $p < 0.0001$, $R^2 = 0.77$).

The median longevity of the wasps raised under each temperature regime is summarized in Table 1. The lifespan of individual wasps ranged between 1 and 9 days. Eleven wasps were still alive after 9 days and were killed, so the longevity data is right censored. The wasps that were reared under intermediate levels of temperature variation (HaLf & LaHf) had the highest mean longevity.

The mean sex ratio (proportion female) of offspring produced by the wasps that developed under the different temperature regimes is summarized in Table 1. The sex ratio of offspring from individual wasps varied greatly from wasps that only produced males to wasps that produced 90% females. We observed a lower proportion of female offspring from the wasps that developed under temperature regimes where daily high temperature peaks occurred, HaHf and LaHf. Excluding those females that produced only males, due to uncertainties of what prevented them from producing males, does not

change the trend. The wasps that developed in temperature regimes with high frequency heat pulses produced proportionally fewer female offspring.

For an overall measure of fitness, i.e. reproductive rate, we calculated Euler's exact r for the wasps reared in each temperature regime (Table 1). The population reared under the least severe environmental conditions (Constant) appeared to have the highest reproductive rate, 4.07, but there were no clear effects of temperature regimes on population level reproduction. Since there was no replication, no further analysis can be done, but this result indicates that the temperature regimes may have little impact on overall population level reproductive rates.

4.5 Discussion

Increases in the amplitude and frequency of extreme warm temperature events, such as those predicted by current global climate change models, can have significant ecological effects (Easterling et al. 2000, Bale et al. 2002). An increase in the occurrence of extreme weather events may negatively affect many organisms, like parasitoids, which fill ecologically and economically important roles in natural and artificial communities. Parasitoids play key roles in the control of many pest organisms and it is important to understand how climate change will influence their life history and fitness, particularly for those species used for commercial biological control purposes.

Immature parasitoid wasps of aphids are subject to the environmental conditions experienced by their host as well as their own thermal stress (Hance et al. 2007). As environmental conditions become more severe, the impact of those conditions (other than direct mortality) should be reflected in the fitness of the resulting adult wasps. It is unclear if immature wasps can acclimate to warmer temperatures, but if they are in fact

able to it may reduce the apparent effects of extreme temperature pulses on the adult parasitoids.

In the treatments that experienced frequent temperature peaks, the development of *A. matricariae* was delayed by up to 3 days (HaHf) (Table 1). Infrequent pulses (2 per week) of 32 or 40 °C did not affect emergence time. If I had measured emergence time more precisely I may have seen delays in development of several hours after experiencing a single heat pulse, similar to Hodson & Gillespie (2010, Unpublished data). The developmental delay can be attributed to the period of time spent above the wasp's developmental threshold, but it could also have been influenced slightly by the lower overnight temperatures used to make all of the temperature regimes average to 23°C.

Delays in development can be costly to individuals for several reasons. An asynchrony between the parasitoid and its host may lead to a decoupling of population dynamics which may reduce the ability for parasitoids to control their host's populations (Hoffmeister and Roitberg 2010). Damage caused by extreme temperatures during development could impact a range of life history traits such as wasp longevity, reproductive ability, egg development, and lifetime reproductive output (Roux et al. 2010, and references within).

This study focused on the impact of extreme and fluctuating temperatures on female wasps only. I did not examine the effects of temperature on males. If the ability of males to mate successfully was reduced after developing under the severe temperature regimes, we could see a reduction in the proportion of females produced by the females we tested because unmated females could only produce male offspring. There are

however, other factors that could lead to the same pattern, such as the ability of female wasps to properly fertilize their eggs, female choice depending on the aphids that she has the opportunity to oviposit into, and male sterility. It appeared that there was a reduced proportion of female offspring produced by the wasps that developed under temperature regimes that featured daily peaks of either 32 or 40 °C and that could be from a combination of any or all of the factors discussed above.

The longevity of the wasps varied widely regardless of the temperature treatment they developed under. There was no clear effect of temperature regime on wasp longevity. Unfortunately, due to a lack of aphid material I was not able to continue the daily oviposition assays for the 11 wasps that were alive after 9 days. After 9 days, the surviving wasps were no longer ovipositing substantial numbers of eggs, and some were not successfully ovipositing at all. Given the right-censored nature of the data, the measures of longevity for two of the five temperature regimes are shorter than they would otherwise be. Roux et al. 2010 found that a single heat shock to an adult female wasp increased mean longevity, but I did not see the same effect when immature wasps experienced either frequent or infrequent periods of high temperature during development.

Increasing the severity of the temperature regimes appeared to have little impact on population level reproductive rates (r) but further repetition of this experiment would be necessary to rigorously analyze the reproductive rates for differences. While performing the experiment it became apparent that the variability in longevity and reproductive output was very high, even though these wasps came from a relatively small gene pool. This variability may be the main reason that the temperature regimes did not

appear to have a large overall impact on parasitoid life history and fitness beyond the observed developmental delay. I performed a power analysis to determine the number of replicates it would require to resolve the number of offspring produced and the longevity. The power to resolve the number of offspring based on temperature treatment was very low at ~ 40% and the power to resolve the wasp longevity was higher at ~ 84%. Unfortunately repeating this experiment several more times (which would likely be necessary to resolve differences in the number of offspring was not a viable option due to the immense workload and time requirements.

There is recent evidence of strong effects of heat shocks on adult *Aphidius* parasitoids (Roux et al. 2010). Roux et al. (2010) found that a single heat shock reaching a maximum temperature of 36 °C not only killed approximately half of the *Aphidius avenae* parasitoids they tested, but it also greatly reduced reproductive output, changed the wasps lifespan, and changed the viability and development rates of the subsequent offspring of the exposed wasps. Although the temperature treatments were directed towards juvenile parasitoids rather than adults it is interesting to note that I did not see the same clear patterns related to wasp lifespan or reproductive output when comparing the results of the wasps that developed under constant conditions to those receiving the temperature pulses. This suggests that the juvenile parasitoids may be capable of dealing with the stresses of extreme heat pulses differently than adult parasitoids.

4.6 Acknowledgements

This work would not have been possible without the help of P. Clarke, L. Hart, and C. Hodson. I would like to thank Dr. Cory for comments on this chapter. Funding for this study was provided by the NSERC Strategic grant held by BDR and DRG.

4.7 Tables

Table 4-1 Life history data for female *A. matricariae* wasps under five heat wave regimes with varying severity. Constant = 23 °C constant, LaLf = 32 °C peaks bi-weekly, LaHf = 32 °C peaks daily, HaLf = 40 °C peaks biweekly, HaHf = 40 °C peaks daily.

Heat wave Regime	Development time (Days)	Median Adult Longevity (Days)	Mean Offspring Produced ± SE	Sex Ratio (Proportion Female) ± SE	Reproductive rate (r)
Constant	12	4	147.00 ± 16.24	0.35 ± 0.058	4.07
LaLf	12	2	142.02 ± 37.96	0.35 ± 0.060	3.78
LaHf	13	6	204.54 ± 32.72	0.15 ± 0.058	3.91
HaLf	12	4	203.07 ± 34.43	0.45 ± 0.058	3.91
HaHf	15	3	131.93 ± 33.03	0.24 ± 0.060	3.92

4.8 Figures

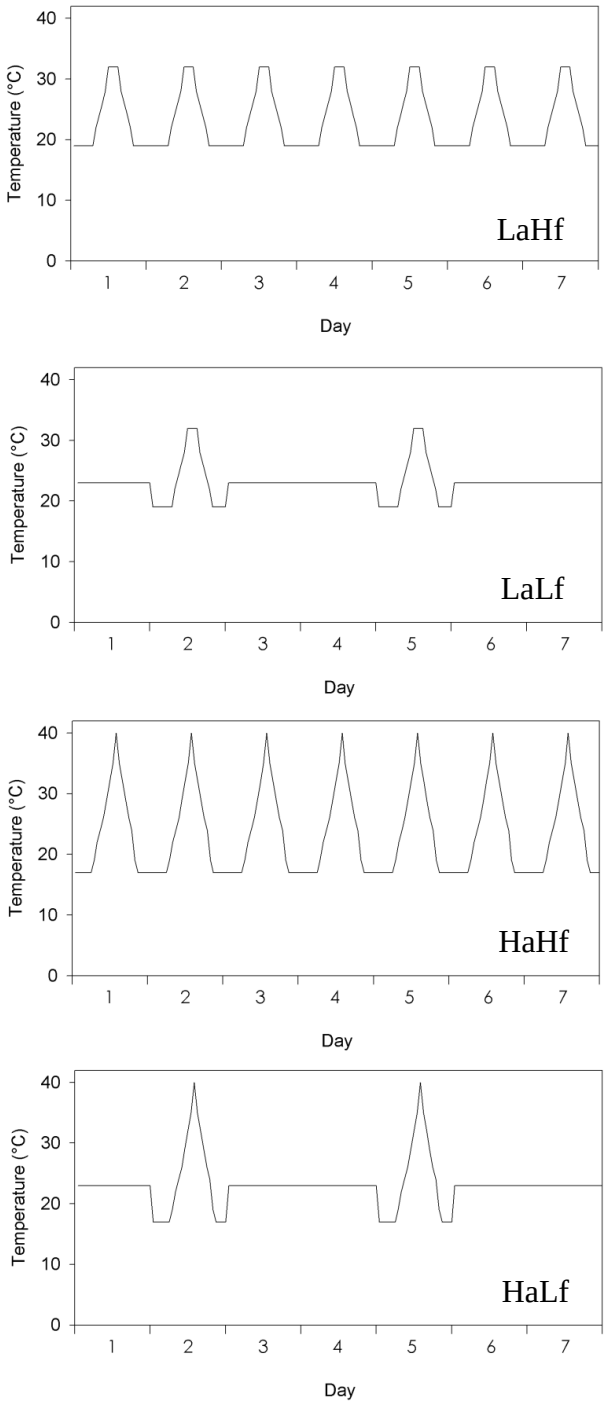

Figure 4-1 Heat wave regimes: 1a = 32 °C peaks daily, 1b = 32 °C peaks bi-weekly, 1c = 40 °C peaks daily, 1d = 40 °C peaks bi-weekly.

4.9 Literature cited

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology **27**:249-268.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. Martijn Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. Hefin Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: Individuals, Populations and Communities. Third edition. Blackwell Science, Oxford.

Cannon, R. J. C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. Global Change Biology **4**:785-796.

Chown, S. L., and J. S. Terblanche. 2007. Physiological diversity in insects: Ecological and evolutionary contexts. Pages 50-152 Advances in Insect Physiology, Vol 33. Academic Press Ltd, London.

Gillespie, D. R., D. J. M. Quiring, R. G. Foottit, S. P. Foster, and S. Acheampong. 2009. Implications of phenotypic variation of Myzus persicae (Hemiptera: Aphididae) for biological control on greenhouse pepper plants. Journal of Applied Entomology **133**:505-511.

Giri, M. K., B. C. Pass, K. V. Yeargan, and J. C. Parr. 1982. Behaviour, net reproduction, longevity, and mummy-stage survival of Aphidius matricariae [Hym. Aphididae]. Entomophaga **27**:147-153.

Hance, T., J. van Baaren, P. Vernin, and G. Boivin. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology **52**:107-126.

Hazell, S. P., B. P. Neve, C. Groutides, A. E. Douglas, T. M. Blackburn, and J. S. Bale. 2010. Hyperthermic aphids: Insights into behaviour and mortality. Journal of Insect Physiology **56**:123-131.

Hodson, C., and D. R. Gillespie. 2010. Effect of a High Temperature Pulse on Development of Aphidius matricariae Mummies. Unpublished data.

Hoffmeister, T. S., and B. D. Roitberg. 2010. The impact of global change on the behavioural ecology of parasitoids. Behavioural Ecology of Insect Parasitoids: a Perspective.

Meehl, G. A., and C. Tebaldi. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science **305**:994-997.

Roux, O., C. Le Lann, J. J. M. van Alphen, and J. van Baaren. 2010. How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid Aphidius avenae (Hymenoptera: Aphidiidae)? Bulletin of Entomological Research **100**:543-549.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science **297**:1292-1296.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Zamani, A. A., A. Talebi, Y. Fathipour, and V. Baniameri. 2007. Effect of temperature on life history of Aphidius colemani and Aphidius matricariae (Hymenoptera : Braconidae), two parasitoids of Aphis gossypii and Myzus persicae (Homoptera : Aphididae). Environmental Entomology **36**:263-271.

5: Conclusion

Global climate change models predict that mean temperatures and temperature variance will increase and that these combined effects will increase the frequency of extreme warm, fluctuating periods of temperature during the summer in temperature regions (Bale et al. 2002, Karl and Trenbeth 2003, Meehl and Tebaldi 2004). An increase in the occurrence of extreme warm summer temperatures will influence development, behaviour, and life history of ectothermic organisms, which in turn will influence species interactions and community dynamics (Huey and Kingsolver 1989, Sibly and Atkinson 1994, Angilletta et al. 2002, Bale et al. 2002, Hance et al. 2007, Roux et al. 2010, Gillespie et al. 2011).

The primary focus of my thesis was to investigate how an increasing frequency and amplitude of severe warm summer temperatures impact ectotherm communities independent of mean temperature effects. I accomplished this by first examining the effects that extreme fluctuating temperatures had on the community dynamics of a theoretical aphid-parasitoid community. I then experimentally investigated how extreme fluctuating temperatures influenced indirect interactions between trophic levels and assessed the direct impact that development under extreme fluctuating temperatures had on the life history of a parasitoid to elucidate how extreme fluctuating temperatures generate the community level impacts that I observed in my model.

In chapter 2, I utilized a stage-structured model to examine the community level impacts of extreme fluctuating temperatures on a model community containing

ectothermic organisms. My goals for the chapter were twofold: first, to determine if stage-structure was useful to model the effects of extreme fluctuating temperatures on a community of ectotherms; and second, to determine the effects of extreme fluctuating temperatures on community dynamics. Although stage-structure was not necessary to describe many of the processes that generated the overall community dynamics, such as the parasitoid's functional response, it was useful to distinguish immature and adult age-classes and to accurately model temperature dependent mortality in the aphid population. In terms of overall community dynamics, daily maximum temperatures, the frequency of extreme warm days, and the autocorrelation of daily temperatures were all found to impact community persistence but the effects of each temperature phenomenon were context dependent. These results support my argument that to fully explain the effects of climate change, additional temperature phenomena should be considered and explored.

Chapter 3 focused on how extreme fluctuating temperatures impacted interactions between parasitoids and their hosts. I found that the reduction in aphid populations through trait-mediated disturbance increased when the frequency and severity of extreme temperatures was increased which suggests that the costs associated with trait-mediated disturbance are likely increased for the hosts under more severe temperature regimes. This result highlights how the effects of extreme fluctuating temperatures extend beyond simple direct effects on each population in isolation. I also found that the amplitude and frequency of the temperature regimes had little impact on the wasp's ability to forage and produce offspring which led to further work which is presented in chapter 4.

In chapter 4 I examined how development under extreme fluctuating temperatures influenced the life history of a parasitoid. I found that development under extreme

fluctuating temperature regimes delayed development time but otherwise had little overall impacts on the wasp's life history. The results discussed in this chapter were only preliminary however, and further, more thorough investigation of the direct effects of extreme fluctuating temperatures will have on insects which fill important ecological and economic roles is necessary.

In each chapter, I show that increasing the frequency and/or severity of extreme temperatures negatively influenced the focal organisms or modified the interactions between species. These findings suggest that extreme and fluctuating temperatures impact communities independently of increased mean temperatures which reinforces my assertion that quantifying the impacts of climate change must extend beyond examining only the effects of changes to mean temperatures.

Further theoretical and experimental studies which explicitly examine how individuals, populations, or communities of ectotherms are influenced by increased frequencies and/or severities of summer temperatures will help to fill a significant void in the current literature which is primarily focused on the effects of increased mean temperatures and the effects of increased winter temperatures in temperate regions.

5.1 Literature cited

Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology **27**:249-268.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. Martijn Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. Hefin Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology **8**:1-16.

Gillespie, D. R., A. Nasreen, C. Moffat, P. Clarke, and B. D. Roitberg. 2011. Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids and two parasitoid species. Oikos ***In Press.***

Hance, T., J. van Baaren, P. Vernin, and G. Boivin. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology **52**:107-126.

Huey, R. B. and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. TRENDS in Ecology and Evolution **4**:131-135.

Karl, T. R. and K. E. Trenbeth. 2003. Modern global climate change. Science **302**:1719-1723.

Meehl, G. A. and C. Tebaldi. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. Science **305**:994-997.

Roux, O., C. Le Lann, J. J. M. van Alphen, and J. van Baaren. 2010. How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid

Aphidius avenae (Hymenoptera: Aphidiidae)? Bulletin of Entomological Research **100**:543-549.

Sibly, R. M. and D. Atkinson. 1994. How rearing temperature affects optimal adult size in ectotherms. Functional Ecology **8**:486-493.

Appendix

1: Predator identity and the nature and strength of food web interactions

Lee M. Henry[1,2], Jordan A. Bannerman[2], David R. Gillespie[2,3]& Bernard D. Roitberg[2] (2010) "Predator identity and the nature and strength of food web interactions," Journal of Animal Ecology, 79, 1164-1171

[1]Zoology Department, University of Oxford, The Tinbergen Building, South Parks Road, Oxford OX1 3PS, [2]Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6 Canada, [3]Pacific Agri-Food Research Centre, Agriculture and Agri-Food Canada, POB 1000 Agassiz, BC V0M 1A0.

This work designed and carried out by J. Bannerman and L. Henry equally. L. Henry wrote the majority of the manuscript, but J. Bannerman wrote parts of the methods section.

1.1 Abstract

1. Most trophic interaction theory assumes that all predators are an abstract form of risk to which prey respond in a quantitatively similar manner. This conceptualization can be problematic because recent empirical work demonstrates that variation in the responses of prey to different predators can play a key role in structuring communities and regulating ecosystem function.

2. Predator identity – the species specific response of prey to a predator - has been proposed as an ultimate mechanism driving the relative contribution of indirect effects in food webs; however few studies have explicitly tested this hypothesis.

3. This study explores the impact of predator identity on direct consumptive (CE) and non-consumptive effects (NCEs), and on the relative contribution of indirect, density and trait-mediated effects in trophic cascades within host-parasitoid communities.

4. We systematically compared the individual, host-parasitoid-plant interactions of two actively foraging parasitoid species with disparate foraging styles, one aggressive and one furtive, a common aphid host and plant. Our results demonstrate that predator recognition and the defensive responses of prey is a critical interaction driving the nature and strength of direct and indirect transmission pathways.

5. Both parasitoid species, in general, had a negative impact on plants. The magnitude of the aphid anti-predator dispersal response was positively correlated with plant infestation and plant damage. The qualitative effect of predator-induced infestation of new plants superseded the quantitative effects of predator-mediated reductions in aphid numbers.

6. The greatest indirect impact on plants was generated by the aggressively foraging parasitoid, and the strength of the aphids anti-predator response (a NCE) antagonistically traded-off with CEs due to an increased investment in attempting to capture risk-sensitized prey. In contrast, the furtive parasitoid did not elicit a strong anti-predator response, had little indirect impact on plants, but generated very high CEs due to the advantage of ovipositing into a sedentary prey population.

7. Our data suggest the responses of prey to different predatory cues may be an important mechanism driving the relative contribution of transmission pathways. We conclude that

predator identity is a key factor influencing the nature and strength of food web transmission pathways.

Keywords: Adaptive behaviour; *Aphelinus abdominalis*; *Aphidius matricariae*; *Aulacorthum solani*; community dynamics; food web; host-parasitoid interactions; indirect effects.

1.2 Introduction

An underlying assumption in most trophic interaction models is that all predators pose threats, to which prey respond in a quantitatively similar manner (e.g. Diehl et al. 2000, Krivan et al. 2004, Peacor et al. 2003, Lima 2002, but see Schmitz et al. 2004). This approach necessarily abstracts the mechanistic details about the ecological interactions among species within food webs. However, this can be problematic because studies have shown that interspecific variation among predators, and even intraspecific variation within a predator species (Post et al. 2008), can have significant impacts on community structure and the regulation of ecosystem function (e.g. Carpenter et al 1987, Pace et al 1999, Peckarsky & McIntosh 1998, Bernot & Turner 2001, Gelwick 2000, Schmitz & Suttle 2001, Schmitz 2008). The importance of individual species interactions in food webs argues for greater effort to uncover the factors driving transmission pathways in order to develop a more comprehensive theory of community dynamics.

The nature of species interactions in ecological communities dictates, among other things, the direct and indirect effects that are transmitted through food webs. In classic population ecology predators ("initiator") directly reduce prey ("transmitter") abundance thereby having a positive effect on the basal resource ("receiver") (e.g. Rosenzweig 1973, Oksanen et al. 1981). Thus the effects generated by direct consumption ("consumptive effects" - CEs) may indirectly influence the basal resource through the reduction of prey density thereby generating density-mediated indirect effects (DMIEs) (Abrams 1995). More recently, studies have shown that predators can also directly cause non-consumptive effects (NCEs) through modifications of prey behaviour, growth or development when in the presence of predators, which can change the way

transmitting and receiving species interact (Abrams 1995, Werner & Peacor 2003, Preisser et al. 2005). Thus predator-induced NCEs may also produce associated indirect effects that are transmitted through trophic levels (i.e. trait-mediated indirect effects TMIEs, see Abrams 2007 for a discussion of terms), which can be additive (positive TMIE) or compensatory (negative TMIE) to the indirect effects generated by direct consumption. In most ecological communities CEs and NCEs operate simultaneously. Therefore, indirect effects associated with the two pathways can be difficult to assess empirically due to confounding interactions between TMIEs and DMIEs (Werner & Peacor 2003 for review). The phenomenon known as a trophic cascade - the indirect effects of carnivores on plants mediated through herbivores – can therefore be driven primarily by a single pathway or a combination of both CEs and NCEs (Okuyama & Bolker 2007), however factors influencing the relative strengths of each pathway are poorly understood.

Schmitz et al. (2004) hypothesized that ultimately trophic cascades may be determined by the behavioural responses of prey to different predators. This hypothesis suggests that there is a continuum of ways that prey respond to different predator species, likely based on the costs and benefits of responding to predators with particular hunting modes i.e., actively-foraging, sit-and-wait and others and foraging domains (Schmitz and Suttle 2001). Under this theory the relative contribution of TMIEs and DMIEs in trophic cascades can be predictable by the hunting mode of the predator. Alternately, prey may be a responding based on the amount of information they have about each predator (i.e. predator identity) and the strength of the prey's response (NCE) is based on the degree of risk aversion to each particular predator species (Bouskila & Blumstein 1992, Sih 1992).

In this study we focus on the role of predator identity in mediating the nature and strength of direct and indirect effects in host-parasitoid communities by controlling for the foraging mode of the predator. We systematically compare the interactions of two different species of actively foraging parasitoids on a common aphid host and basal resource. The foxglove aphid, *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae), is a phloem feeding insect that causes extensive leaf curling, chlorosis, and impedes plant growth, and has several adaptive behavioural defenses, including a predator-induced dispersal response. Both parasitoids are widely distributed, natural enemies of the foxglove aphid and are indigenous in the native range of *A. solani* (Takada 2002, Mackauer & Stary 1967). *Aphidius matricariae* (Haliday) (Hymenoptera: Aphidiidae) is an aggressive parasitoid that has a quick sting (<1sec), can sting moving hosts, and elicits a strong anti-predator response in aphids resulting in dispersal (NCE). In contrast, *Aphelinus abdominalis* (Dalm.) (Hymenoptera: Aphelinidae) uses a furtive form of attack. It cautiously moves through aphid patches, has a much slower sting (>1min), requires a sedentary host in order to oviposit, and elicits a very weak anti-predator dispersal response in aphids. This model system allowed us to investigate the impact of predator identity on transmission pathways with predators that occupy the same guild and foraging habitat, but are recognized and responded to differently by the aphid host (transmitter species). Our goals for the current study were to:

1) Quantify the variation in direct consumptive and non-consumptive effects when aphids are exposed to natural enemies with different foraging strategies.

2) Determine the influence of predator identity (i.e. predator-based cues and causes) on the nature, strength and relative contribution of indirect effect pathways in trophic cascades.

1.3 Methods

This study draws from three experiments that breakdown the behavioural and community level interactions causing trophic cascades in aphid-parasitoid systems. The first experiment quantifies the behavioural response of an aphid species when exposed to parasitoids with different foraging styles, one aggressive and one furtive, using small patches of aphids exposed to single parasitoid females. A second experiment explores how the differences in behavioural responses of the prey impact direct and indirect species interactions at a community level using a mesocosm experiment. An additional behavioural experiment demonstrates how the degree of predator-induced prey risk-sensitization in prey (NCE) can influence the opportunity for predation (CEs) and therefore the relative contribution of effects (i.e. trait- or density- mediated) causing trophic cascades.

1.3.1 Maintenance of insect colonies

Foxglove aphids were collected from commercial pepper greenhouses (Abbotsford, British Columbia) and maintained on excised leaves of sweet pepper, *Capsicum annuum* L. (Bell Boy, Stokes Seeds St. Catherines, ON, Canada), in 500 ml plastic cups in the laboratory for one-month prior to the start the experiment to allow the aphids to acclimate to laboratory conditions. *Aphidius matricariae* and *A. abdominalis* were reared on *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) feeding on pepper.

Parasitoids emerged in glass jars, and were allowed 1-4 days (depending on parasitoid species) to mate and acclimate to laboratory conditions. All experimental insects were maintained at 20 ± 2 °C and a 16L:8D photoperiod. Test parasitoids were always 1-2 day old *A. matricariae* and 2-4 days old *A. abdominalis* (ages based on female responsiveness to aphid hosts, D. Gillespie personal observation) naïve females (no contact with hosts prior to experiment) that had been given continuous access to a 10% honey solution, water and males. Sweet pepper, cv. Bell Boy, was used as a basal resource in all experiments.

Predator identity and non-consumptive effects - quantifying A. solani defensive behaviour

We determined the influence of parasitoid foraging behaviour on the strength of the anti-predator dispersal response in aphids (i.e. a NCE). The response of aphids was examined at the aphid-patch level. A single female parasitoid was transferred into a 50 x 9mm Petri dish (FALCON®, Franklin Lakes, NJ) containing a 2 cm diameter leaf disc with 5-10 aphids of mixed instars. Each parasitoid was allowed to oviposit in a single aphid in the patch, and the patch response was recorded. Patch-level responses were: no disruption (no aphids moved); local (only the stung aphid was disrupted and emigrated); patch (the stung aphid plus at least one neighboring aphid dispersed); and global disruption (stung aphid produced alarm pheromone, resulting in a global aphid dispersal response). Aphids were considered dispersed if they left the leaf disc, which in most natural scenarios would result in the aphids dropping off the plant. A Chi-square test was used to analyze differences in the proportion of aphid patch responses when exposed to each parasitoid species.

Variation in physiological ability to parasitize A. solani

The probability of parasitism following a single oviposition was assessed. Parasitoids were allowed to sting an aphid once, and the aphid was then transferred into a rearing cup where the outcome of the parasitism event was recorded (mummy formation, aphid deceased or aphid alive). This was repeated 49 and 52 times for *A. abdominalis* and *A. matricariae* respectively and analyzed across species using a Chi-square.

1.3.2 Influence of parasitoid foraging behaviour on direct and indirect effects

Experimental setup, treatment structure, and data collection

Experiments on the impacts of predator identity on species interactions and trophic cascades were performed in 0.61m^2Bugdorm® cages (BioQuip, Rancho Dominguez, CA). Uniform plots of plants were established by transferring 49, three-week old pepper plants into square (7 x 7 cell) plant trays (one plant per cell). Plots were fertilized with 1% W/V, 20-20-20 water soluble fertilizer, and allowed to grow for an additional three days under HPS lights 16L:8D photoperiod in cages, after which caged plant plots were dispersed in three experimental rooms. The rooms were maintained at a 16L:8 D photoperiod using a mix of GE® plant and aquarium fluorescent bulbs and normal fluorescent bulbs at a temperature of 20±3°C. Four cages were housed in each room. The experiment was completely randomized within room and blocked by room so that each room had an equal number of replicates of each treatment (N=6) over three repeats in time.

Experimental treatments were: plants without aphids, plants with aphids only, plants with aphids and *A. matrcariae* females, and plants with aphids and *A. abdominalis*

females. A cue treatment for each parasitoid species simulated parasitoid foraging, but without female parasitoids, thus controlled for CEs and DMIEs.

The cue treatments received disturbances to simulate parasitoid foraging that were based on the aphid anti-predator response laboratory assays. The presence of *A. abdominalis* was simulated by gently prodding the aphid's abdomen with the blunt end of an insect pin (5-10 aphids, each on separate leaves), twice daily, which resulted in local or patch level aphid disruption. Prodding 5-10 aphids twice daily was also used to simulate the presence of *A. matricariae*, and an additional four 2nd instar aphids (from an outside source) were pinched behind the head with a pair of fine tip forceps to release alarm pheromone, killed and placed near aggregations of aphids producing large, long lasting signals of the presence of a predator that caused most of the aphids on a plant to disperse (i.e. global disturbance). Male parasitoids of each species were added to both cue treatments to produce physical disruption through aphid contact; males forage for females on host plants in a manner similar to female parasitoids.

At the start of each trial, one hundred foxglove aphids (approximately 50 juveniles and 50 adults) were transferred to small pepper leaves in individual cups. After all aphids had settled (~24 hours) the aphids (and leaf) were carefully placed on the central plant of each plot. The following day, in the parasitoid treatments, five parasitoids were released under the central plant. To maintain foraging activity, the parasitoids were removed and five new parasitoids were released under the central plant every three days. This ensured parasitoids maintained consistent foraging activity, irrespective of species (parasitoids were all at their peak foraging age), over the course of the experiment. All female parasitoids were allowed to sting a single foxglove aphid

prior to release to acclimate the parasitoids to the host species as well as to ensure the females were actively foraging. Male parasitoids were acclimated to foxglove aphids in a similar manner. Trials were stopped after 10 days as the plots was only large enough to maintain the rapid reproduction of aphids without saturating the plants and to control for the population of parasitoids, as after 10 days the new generation of parasitoids would emerge thus confounding predator densities.

Parasitoid-aphid-plant interactions

The number of plants infested, and the number of aphids on each plant was recorded on each of the first 3 days and then every other day until the 10^{th} day. Counts were performed before the first of the two daily disturbances was applied to the cue treatments. Aphid emigration was assessed using the numbers of plants infested over the first 3 days of the experiment. This measure of dispersal was analyzed from the initial point infestation to day 3 only in order to examine aphid emigration due to the anti-predator response of aphids, while controlling for emigration due to crowding (numbers of aphids, and thus dispersal due to crowing, differed between treatments past day 3). Aphid dispersal and population size were analyzed with a Generalized Linear Model using a GENMODE procedure (SAS, 1999). An additional, generalized estimating equation (GEE) was included with an AR1 correlation to account for repeated measures of experimental units over time. Variables for dispersal included the number of plants infested, time and the interaction between number of plants infested and time. Variables for aphid population size included the number of aphids per plot, time, and the interaction between population size and time. A Poisson distribution with a log link function was

used for both dispersal and population size (the scale parameter "dscale" was estimated by the square root of "deviance/degrees of freedom").

Aphid aggregation (*J* index, Ives 1988) was used to measure differences in aphid movement between treatments over 10 days:

$$J = (s^2/\overline{x} - 1) / \overline{x} \qquad \text{Equation 1}$$

Where $\overline{x}$ = mean aphids per plant in each sample plot and s^2= plot variance. The *J* index is similar to other commonly used aggregation indices, but it is less vulnerable to biases through differences in density or sample size (Rohlfs & Hoffmeister 2004). *J* values were compared across treatments over time to determine the differences in aggregation using repeated measures MANOVA (correction for sphericity violation as in O'Brien, R.G. & Kaiser 1985). *J* values are predicted to decrease (become less aggregated) over time in all treatments as aphids reproduce and spread from a point infestation to the finite number of plants in each plot.

The influence of parasitoid species on aphid-plant interactions was investigated through the total number of plant-infested days (PID), which is the sum of the total number of plants infested on each sample day, over the course of the experiment.

$$\text{PID} = \sum_{i=1}^{10} (\#\ of\ plants\ infested)_i \qquad \text{Equation 2}$$

Where *i* is the days that the number of infested plants were sampled. Total plant-infested days were analyzed across treatments using ANOVA.

On day 10 all aphids from each of the plots were counted and those from the plots containing parasitoids were transferred into rearing cups. Aphids were maintained in these cups with fresh leaves supplied as needed until all of the parasitized aphids had formed mummies (parasitoid larvae pupation), thus generating a measure of direct consumption of aphids by each parasitoid species. The number of mummies per treatment was analyzed with ANOVA.

Cascading trophic interactions

The indirect impact of parasitoids on plant growth, transmitted through the aphids, was compared across treatments. On day 10 the number of plants showing signs of aphid damage was recorded. Removing and photographing all the leaves from each plot then using the area function in Sigma Scan Pro 5.0 was used to calculate leaf area. Due to the large number of leaves, area was determined for the 1st true leaves only. This sub-sample accurately represented foxglove aphid damage as the damage from the aphid is systemic, and occurs while the plant is developing, thus damaging the entire plant. Additionally, all above ground plant parts in each plot were combined, dried and weighed to obtain total dry plant biomass. Total number of plants damaged, leaf area and plant biomass were analyzed across treatments using ANOVA, blocking for room, to control for variation generated by the separate rearing rooms. Two replicate plots were removed from the study due to unhealthy plants prior to the addition the aphids.

1.3.3 Non-consumptive effects and the opportunity to oviposit

The impact of predator identity on a parasitoid's opportunity to oviposit was examined as a possible mechanism influencing the relative strength of direct and indirect

effects in this system. This experiment also addressed an important antagonistic interaction between the transmission pathways observed in the mesocosm experiment: the NCE can reduce CEs through reduced opportunity to oviposit when prey express anti-predator traits. A patch of 10 aphids on a 2 cm diameter leaf in a Petri dish was exposed to either *A. matricariae* or *A. abdominalis* for 2 min, beginning after the first oviposition. After this first foraging period the parasitoid and any aphids that dispersed from the leaf as a result of the parasitoid attack were removed. The remainder of the patch was then exposed to a second parasitoid of the same species for a further 2 min. Loss of opportunity, and thus the potential to generate direct CEs, was measured by the reduction in the number of prey due to the adaptive anti-predator response after each 2-minute period. The number of aphids receiving an oviposition was also recorded in each foraging event. The difference in the number of aphids escaped due to the anti-predator dispersal response as well as the difference in number of ovipositions from the first foraging bout to the second was analyzed across parasitoids using paired *t*-tests.

Analyses were performed using JMP 7.0.2 statistical software, except for the GEE analyses which were performed in SAS 8.2 (SAS Institute, Cary, NC, USA).

1.4 Results

1.4.1 Interspecific variation in aphid-parasitoid interactions

Predator identity and non-consumptive effects- quantifying A. solani defensive behaviour

The anti-predator dispersal response (NCE) was greater when patches of aphids were attacked by *A. matricariae* compared to those attacked by *A. abdominalis* (n = 89, $\chi^2_{(3)} = 33.24$, $p < 0.0001$). When attacked by *A. matricariae*,6% of aphids did not

respond, 34.7% responded locally by moving away from the parasitoid, 30.4% of attacks resulted in the aphid patch being disrupted and 28.2% produced alarm pheromone resulting in a global dispersal. When attacked by *A. abdominalis* 44.1% of the aphids did not respond, 46.5% responded locally, 6.9% of attacks disrupted the patch and 2.3% (one attack) produced global dispersal.

Variation in physiological ability to parasitize A. solani

The outcome of a single oviposition did not differ between the two parasitoid species (n = 101, $\chi^2_{(2)} = 0.073$, p = 0.96), demonstrating there was no difference between parasitoids in the physiological ability to parasitize foxglove aphids. In 49 aphids attacked by *A. abdominalis*, 29% were parasitized, 19% were dead, and 52% were alive. In 52 aphids parasitized by *A. matricariae*, 27% were parasitized, 20% were dead and 53% were alive.

1.4.2 Influence of parasitoid foraging behaviour on direct and indirect effects

Parasitoid-aphid-plant interactions

Aphid dispersal was estimated through the number of plants that became infested over the first three days of the experiment (Fig 1). *A. matricariae* and *A. matricariae* cue lead to a rapid increase in the plant infestation rate over the first 24 hours (GEE days 0-1 treatment*time $\chi^2_{(4)} = 17.50$, p = 0.0015) compared to *A. abdominalis* cue, *A. abdominalis* and the aphids only treatment. Over 3 days there was a significant difference in the number of plants infested between treatments ($\chi^2_{(4)} = 9.67$, p = 0.04) with *A. matricariae* and *A. matricariae* cue maintaining higher numbers of infested plants

compared to all other treatments, however the rate of infestation was not different across treatments beyond the first day ($\chi^2_{(4)}$ = 3.18, p = 0.53). Plant infestation did not differ between *A. matricariae* and *A. matricariae* cue (treatment $\chi^2_{(1)}$ = 1.30, p = 0.25; treatment*day $\chi^2_{(1)}$ = 1.13, p = 0.28) or between *A. abdominalis* and *A. abdominalis* cue (treatment: $\chi^2_{(1)}$ = 3.48, p = 0.062; treatment*day; $\chi^2_{(1)}$ = 0.45, p = 0.50). Thus, both cue treatments were accurately mimicking the respective, anti-predator dispersal response of the aphids. The number of infested plants was higher in the *A. matricariae* treatment compared to the *A. abdominalis* treatment ($\chi^2_{(1)}$ = 5.50, p = 0.02), demonstrating that the aphids identified and responded to the different parasitoid species by varying the magnitude of their anti-predator dispersal response.

Aphid aggregation (*J*-index) differed among treatments over 10 days (MANOVA: treatment $F_{4,15}$= 98.36 p <0.0001; time $F_{6,10}$ = 40.40 p < 0.0001; treatment*time $F_{24,36.1}$= 3.77 p = 0.0002) (Fig 2a). As predicted all treatments became less aggregated with time. The aphid-only treatment was the most aggregated, *A. abdominalis* generated an intermediate aphid aggregation and *A. matricariae's* presence resulted in little to no aphid aggregation. Cue treatments were different from corresponding parasitoid treatments. Independent contrast analysis demonstrated that aphids were more aggregated when exposed to *A. abdominalis* compared to *A. matricariae* (treatment: $F_{1,15}$= 4.47 p = 0.016), and that aggregation between them differed over time (time*treatment: $F_{6,10}$= 4.47, p = 0.019). Both parasitoid treatments differed from the aphid only treatment (*A. abdominalis*: $F_{6,10}$= 10.29, p = 0.0009; *A. matricariae* $F_{6,10}$ = 25.07, p < 0.0001).

Aphid population size differed among treatments over time (treatment: $\chi^2_{(4)}$ = 10.34 p = 0.035; treatment*day; $\chi^2_{(4)}$ = 13.42, p = 0.0094). There were two distinct

groups: the two cue treatments and the aphid only treatment formed one group; and the *A. abdominalis* and *A. matricariae* treatments formed a second (Fig 2b). In the former, aphid numbers increased exponentially, whereas in the latter, numbers remained approximately the same as the starting numbers.

The cumulative plant-infested days (PID) differed between treatments (ANOVA: treatment $F_{4,23}$= 5.12, p = 0.004). Tukey HSD indicated that *A. matricariae* and *A. matricariae* cue generated significantly greater plant-infested days (159.83 ± 15.1 and 173.83 ± 12.6, respectively) than the aphid-only treatment (99.83 ± 9.5), whereas *A. abdominalis* and *A. abdominalis* cue did not (132.22 ± 14.4 and 127.5 ± 12.4, respectively).

Direct consumption of aphids, as indicated by the number of parasitoid mummies, was much greater in *A. abdominalis* (77.3±11.9) than *A. matricariae* (26.57±12.7)($F_{1,13}$ = 8.47 p = 0.012).

Cascading trophic interactions

The number of plants showing aphid damage at the end of the experiment differed among treatments (ANOVA: $F_{4,23}$= 37.63 p < 0.0001). The *A. matricariae* and *A. matricariae* cue treatments indirectly caused the greatest number of plants to be damaged, *A. abdominalis* and *A. abdominalis* cue had moderate levels of plants damaged and the aphid treatment had the lowest plants damaged (Table 1). There was no room effect on the number of plants damaged (ANOVA: $F_{2,23}$= 3.11 p = 0.10).

Leaf area and plant biomass were significantly reduced in several treatments (ANOVA: area $F_{5,17}$= 3.12 p = 0.013; biomass $F_{5,17}$= 3.32 p = 0.03). However, both

proxies were also influenced by room (area $F_{2,17}$= 8.99 p = 0.0016; biomass $F_{2,17}$= 17.04 p = 0.0001) and plants in one room were consistently smaller than in the other two. Due to the large effect of room on leaf area and biomass, and because there was not a significant interaction between room and treatment (area $F_{10,17}$= 1.58 p = 0.19, biomass $F_{10,17}$= 1.4 p = 0.26), all replicates from the room that had reduced growth were removed and the analysis was repeated on a subset of the data. Exclusion of the one room removed the room effect (area $F_{1,15}$= 0.028 p = 0.87. biomass $F_{1,15}$= 1.54 p = 0.22). Treatment influenced leaf area ($F_{5,15}$= 4.31 p = 0.012) and plant biomass ($F_{5,15}$= 3.07 p = 0.039) Leaf area and plant biomass were lowest in the *A. matricariae* and *A. matricariae* cue treatments, followed by *A. abdominalis* and *A. abdominalis* cue, the aphid only treatment, and greatest in the plants only treatment (Table 1). Only the *A. matricariae* and *A. matricariae* cue treatments differed in leaf area from the aphid only and plants without aphids treatments.

1.4.3 Non-consumptive effects and the opportunity to oviposit

Parasitoid species differed in the reduction of available prey due to the anti-predator dispersal response of aphids over consecutive foraging events (paired *t*-test: $F_{1,18}$ = 21.42 p = 0.0002). Exposure to the first *A. matricariae* resulted in an average of 97% ± 2% aphids escaping (1.9 ± 0.27 aphids stung), reducing to 99% ± 1% (0.3± 0.15 aphids stung) after the second foraging event. In contrast, only 22% ± 6% escaped from the first *A. abdominalis* foraging bout (1.5 ± 0.22 aphids stung), reducing to 43% ± 9% escaped on the second foraging bout (1.9 ±0.27 aphids stung). The cumulative number of ovipositions across foraging bouts also differed between parasitoid species ($F_{1,18}$ = 7.30 p = 0.014), with *A. abdominalis* ovipositing in a greater proportion of the aphid patch over

successive bouts (0.34 ± 0.03) compared to *A. matricariae* (0.22 ± 0.03). This demonstrates that there is a substantial decrease in oviposition opportunity for subsequent *A. matricariae* females due to the displacement of aphid hosts caused by the initial female's induction of a strong NCE. In contrast, there is little difference in opportunity between foraging bouts of *A. abdominalis.*

1.5 Discussion

Our results demonstrate that the response of prey to different predators is a critical interaction governing the nature and strength of food web transmission pathways. The magnitude of the aphid's anti-predator response (NCE) differed substantially in the presence of the two parasitoid species at both the plot level (Fig 1) and the patch level. Parasitoid species directly influenced aphid aggregation (Fig 2a), and indirectly influenced the number of plants infested by inducing aphid dispersal, resulting in a positive correlation between the magnitude of the NCE and resource exploitation by the herbivore. Subsequently, plant fitness (Table 1) was reduced by the cumulative number of plants infested over the course of the experiment. The strength of the NCE caused an equivalent negative cascading effect. This suggests a tight correlation between the magnitude of the prey's adaptive anti-predator response (a NCE) and the reduction in plant fitness (a TMIE) in this system. This result demonstrates that the magnitude of a prey's response to different predator species can play a critical role in determining the consequences of species interactions.

Plant damage did not differ between cue and non-cue treatments, which controlled for CEs (Table 1). Aphid numbers were reduced in the presence of female parasitoids

(Fig 2b), demonstrating that CEs were occurring. However, there was no correlation between aphid numbers and plant damage suggesting that the magnitude of the anti-predator response of the aphids dictated the number of plants infested, and was the primary determinant of the observed cascading effect. Therefore the indirect effect of parasitoids on plants was primarily a TMIE not a DMIE. This result does not preclude the importance of DMIEs within aphid parasitoid system, as DMIEs typically manifest over longer time frames as individuals are removed from the population by predation (Werner & Peacor 2003). However, due to the explicit sequence of events of NCEs (i.e. dispersal and plant infestation) followed by CEs we would predict that relatively large NCEs in aphids, such as when dispersing from *A. matricariae* attacks, would always coincide with greater degrees of TMIEs due to a spatially greater amount of plants infested by the aphids dispersing from a focal point. Although, DMIEs did not contribute much to the net indirect effects of parasitoids on plants under our experimental time frame, *A. abdominalis*, on average, parasitized 47.9% and *A. matricariae* 24.0% of the aphid population. It is possible that over longer time periods *A. abdominalis - A. solani* interactions could result in a shift in the relative contribution of indirect transmission pathways that may even reverse the sign of the cascading interaction (Werner & Peacor 2003). This is due to a reduced anti-predator response (NCE) in the aphids when attacked by *A. abdominalis* allowing for a significant removal of the non-risk sensitized aphids by predation while minimizing plant infestation, and subsequent plant damage (TMIE), caused by predator-induced aphid dispersal. Our results suggest that DMIEs caused by CEs maybe more prevalent when there is minimal amounts of predator-induced risk-sensitization in prey (e.g. *A. abdominalis - A. solani*), where as increasing

predator-induced disturbance and prey risk-sensitivity is likely to coincide with a greater relative contribution of TMIEs (e.g. *A. matricariae* - *A. solani*). The relative contribution of trait- and density mediated effects causing trophic cascades may therefore be governed primarily by the interplay between prey risk-assessment and predator foraging style (i.e. predator identity) as opposed to specific foraging modes of predators as previously suggested (Schmitz O. & Suttle 2001).

The difference in direct CEs from parasitism between the two parasitoids was surprising, given that there was no difference in the probability of parasitism between the two parasitoid species when ovipositing in a single aphid. This discrepancy suggested that a mechanism exists that affords *A. abdominalis* a greater capability to impose CEs through parasitism than *A. matricariae,* and therefore this type of predator-prey interaction also has the potential to generate greater DMIEs. We showed that the strength of the anti-predator response can dramatically impact future opportunity for predation and that a strong NCE displaces prey through dispersal or hiding thereby removing opportunity for subsequent predators. Parasitoids in particular could suffer substantial time and energy costs from predator-sensitized prey due to their reliance on herbivore-induced plant volatiles to locate hosts, and is the likely reason *A. matricariae* has a relatively reduced parasitism rate in the mesocosm experiment. Predators that generate a strong NCE, like *A. matricariae,* must invest more time in locating and/or capturing sensitized prey, which reduces the potential to impose CEs and any indirect effects associated with directly reducing the prey population through parasitism or predation. In contrast, predators with a furtive foraging style, such as *A. abdominalis*, that do not induce a strong anti-predator response gain a relative advantage in exploiting prey as a

resource. Thus an antagonistic interaction exists between the strength of a NCE and the potential to generate CEs (and potentially DMIEs) that is directly related to the way in which prey identify and respond to different predator species. Previous studies have suggested that a significant portion of the net effects of a predator may be attributed to an interaction between predator and prey densities and NCEs (reviewed in Werner & Peacor 2003). Our data demonstrates that NCEs may displace CEs, and subsequently influence the relative contribution of indirect effects in trophic cascades. This result has substantial implications for the relative contribution of transmission pathways in ecological communities as prey species reduce exposure through predation-related risk-aversion in many terrestrial (e.g. Messina 1981, Beckerman et al. 1997) and aquatic systems (e.g. McIntosh & Townsend 1996, Peckarsky & McIntosh 1998, Gelwick 2000).

Indirect effects are thought to play a large role in structuring aphid-parasitoid communities (Muller & Godfray 1999). Our data suggest that the qualitative effects of predator-induced plant infestation actually supersede the quantitative effects of a reduction in aphid density. In addition, aphids are known vectors of many plant viruses so the qualitative effects of aphid-natural enemies interactions may indirectly impact plants by both mediating plant infestation rates by aphids and subsequently disease transmission in plants. Studies have shown that the dispersal response of aphids exposed to natural enemies that elicit strong antipredator behaviour, such as ladybird beetles (*Coccinella califonica*), is correlated with an increased spread of Bean Yellow Mosaic Virus (Roitberg & Myers 1978) and Barley Yellow Dwarf Virus (Smyrnioudis et al. 2001). Adaptive movement of prey in response to predation is also thought to be an important factor in metapopulation dynamics (Abrams 2008). The adaptive response of

pests to different predator species is therefore an important factor dictating rates of infestation and spatial impact of economically important pest species. These results add to the growing body of literature that suggests predator identity as an important factor in prey suppression (Schmitz & Suttle 2001, Chalcraft & Resetarits 2003) especially in biological control (Straub and Snyder 2006, Denoth et al. 2002).

Studies involving multiple predators and the same prey in a single system have provided insight into the role different predators play in resource consumption and in the structuring of ecological communities (Sih et al. 1998, Peckarsky & McIntosh 1998, Bernot & Turner 2001, Gelwich 2000), however these generally do not address the relative contribution of effect pathways. In a study of species interactions among hunting spiders, a single grasshopper species and two plant species in an old-field food web Schmitz & Suttle (2001) demonstrated that spiders with different hunting modes elicited very different direct and indirect effects in prey, and on the basal trophic level. The relative contribution of pathways within this system ranged from primarily NCEs in the sit-and-wait predator to strictly CEs in the actively foraging spider. The authors concluded that the foraging mode of the predator was likely the primary factor driving transmission pathways (Schmitz & Suttle 2001). Our results strongly support the hypothesis that ultimately trophic cascades are determined by behavioural responses of prey to different predators (Schmitz et al. 2004). However, our results clearly show that even within predators that share the same foraging mode (i.e. both active foragers) and forage in the same microhabitat there can be considerable variation in the strength and nature of direct and indirect effects. In our study the most aggressive forager, *A. matricariae*, caused the greatest indirect impact on plants with the strength of the NCE

antagonistically trading-off with the capability to directly generate CEs. In contrast the furtive forager, *A. abdominalis*, caused a lesser NCE and a higher CE. Thus the nature and strength of direct and indirect effects may primarily depend on the responses of prey to different predatory cues, not necessarily on specific predatory hunting modes or foraging habitats as this amalgamation of species may conceal the fundamental mechanisms responsible for the structure and stability of ecological communities.

1.6 Acknowledgements

The authors thank P. Clarke, F. Simon, M. Anaka, J. Dubman and Z. Monteith for assistance with experiments. We would also thank C. Dean and T. Hoffmeister for statistical advice and NSERC Strategic Grant STPGP 350434 for funding this project.

1.7 Tables

Table A-1-1 Mean number of plants damaged, leaf area and plant biomass in 49 pepper plants in plots following exposure to treatments with and without aphids, parasitoids. Superscript letters indicate significant differences between treatments.

	Mean number of plants damaged	Mean leaf area	Mean plant biomass
Plants without aphids	0	1427.7 ± 151.6 [a]	4.19 ± 0.29 [a]
Aphids	12.5 ± 1.55 [a]	1355.3 ± 43.2 [a]	3.83 ± 0.09 [a]
A. abd	30.3 ± 1.7 [b]	1051.2 ± 89.0 [a,b]	3.32 ± 0.18 [a]
A. abd C	28.0 ± 2.9 [b]	1201.8 ± 77.9 [a,b]	3.32± 0.25 [a]
A. mat	45.0 ± 1.7 [c]	1004.4 ± 34.5 [b]	2.86 ± 0.37 [a]
A. mat C	42.5 ± 2.1 [c]	1010.9 ± 61.2 [b]	2.94 ± 0.44 [a]

1.8 Figures

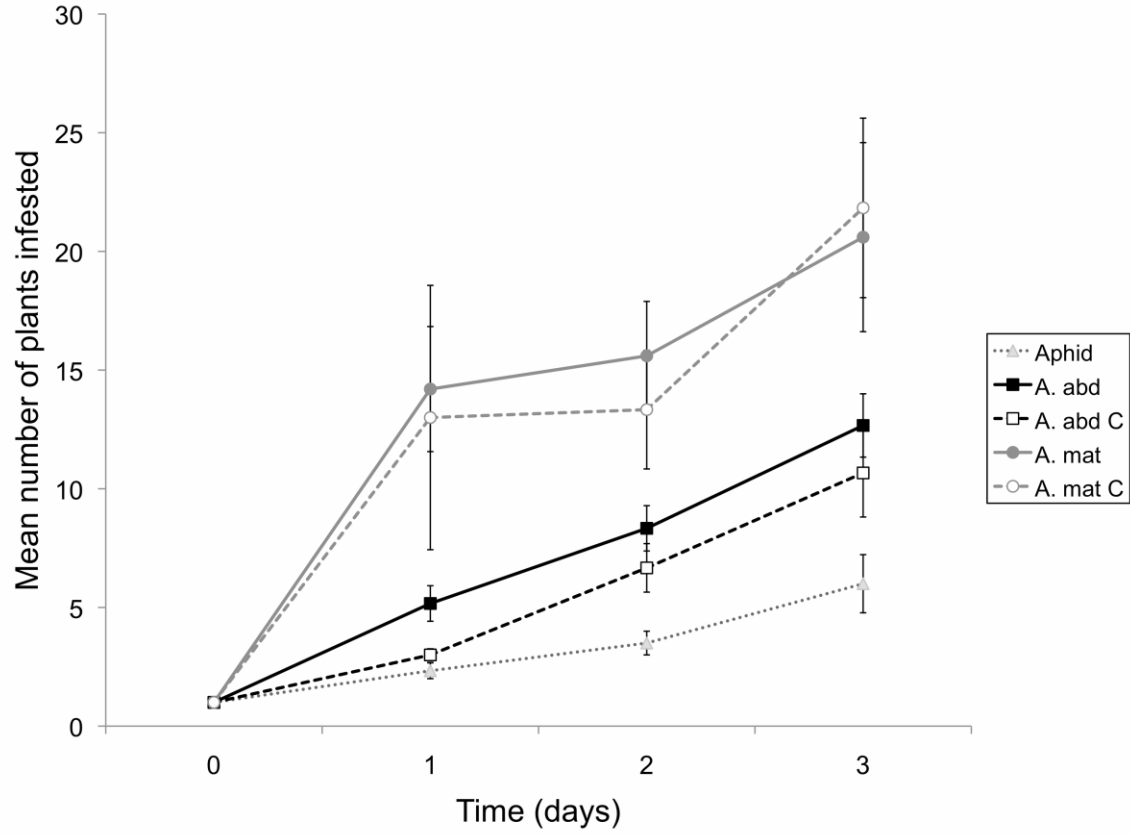

Figure A-1 Effect of parasitoid treatments on plant infestation in caged mesocosm experiments. Treatments were *A. abdominalis* (A. abd), *A. matricariae* (A. mat), aphids only (A) or cue treatments that simulate either *A. abdominalis* (A. abd C) or *A. matricariae* (A. mat C).

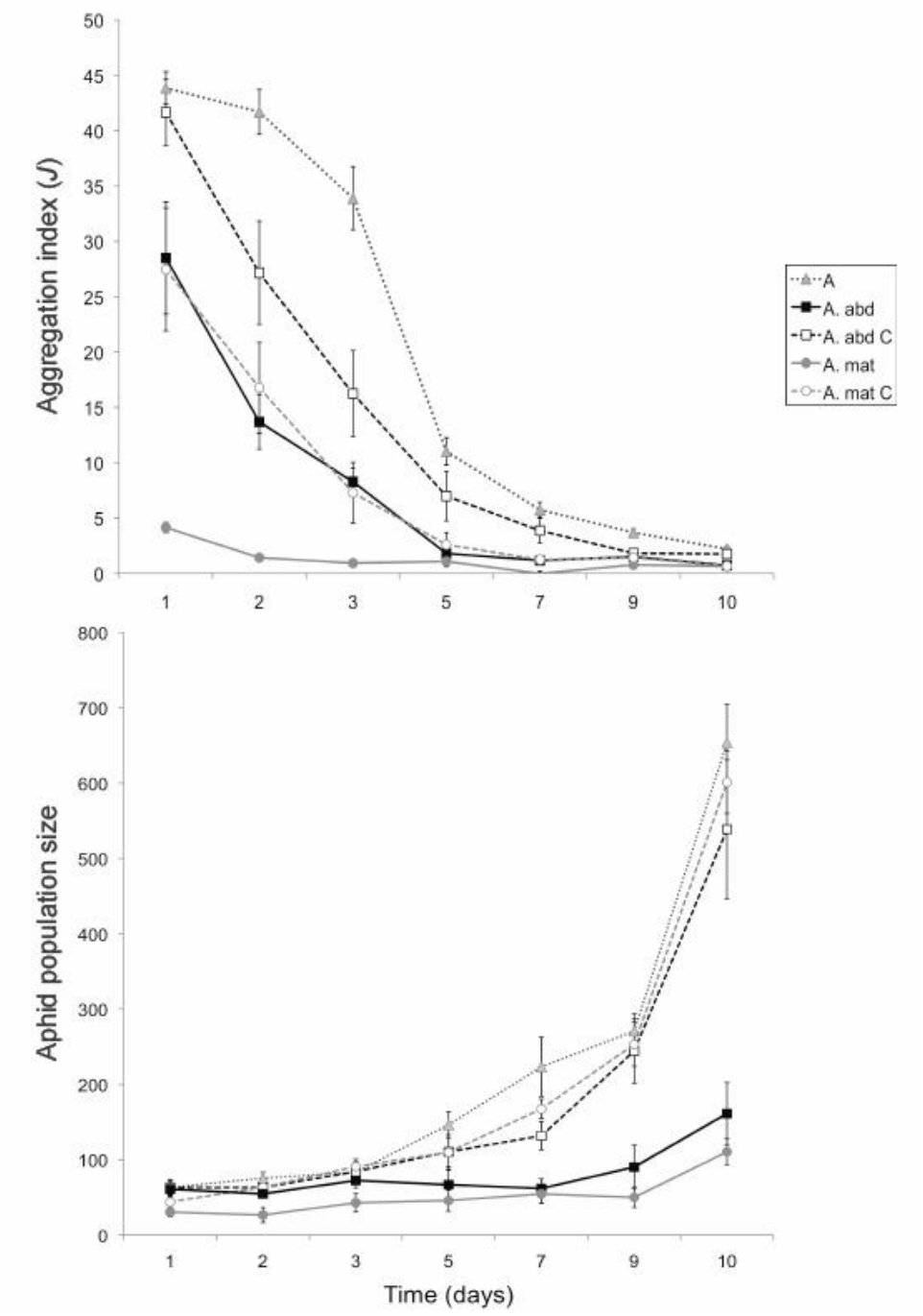

Figure A-2 Effects of parasitoid treatment on aphid aggregation and aphid population size in caged mesocosm experiments. 2a. Mean index of aphid aggregation over the full 10-day experiment. 2b. Mean aphid population size over the full 10-day experiment. Treatments were *A. abdominalis* (A. abd), *A. matricariae* (A. mat), aphids only (A) or cue treatments that simulate either *A. abdominalis* (A. abd C) or *A. matricariae* (A. mat C).

1.9 Literature Cited

Abrams, P. (2008). Measuring the population-level consequences of predator-induced prey movement. *Evolutionary Ecology Research,***10**, 333-350.

Abrams, P. (2007). Defining and measuring the impact of dynamic traits on interspecific interactions. *Ecology*, **88**, 2555-2562.

Abrams, P. (1995). Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist*, **146**, 112-134.

Beckerman, A., Uriarte, M. & Schmitz, O. (1997).Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Acadamy of Science of the United States of America*, **94**, 10735-10738.

Bernot, R. & Turner, A. (2001). Predator identity and trait-mediated indirect effects in a littoral food web. *Oecologia*, **129**, 139-146.

Bouskila, A. & Blumstein , D. (1992). Rules of thumb for predation hazard assessment - predictions from a dynamic model. *American Naturalist*, **139**, 161-176.

Carpenter, S., Kitchell, J., Hodgson, J., Cochran, P., Elser, J., Elser, M. et al. (1987). Regulation of lake primary productivity by food web structure. *Ecology*, **68**, 1863-1876.

Chalcraft, D. & Resetarits, D. (2003). Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology*,**84**, 2407–2418.

Denoth, M., Frid, L. & Myers, J.(2002). Multiple agents in biological control: improving the odds? *Biological Control*,**24**, 20–30.

Diehl, S., Cooper, S., Kratz, K., Nisbet, R., Roll, S., Wiseman, S. et al. (2000). Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *American Naturalist*, **156**, 293-313.

Gelwick, F. (2000). Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. *Oecologia*, **125**, 573-583.

Godfray, H. & Shimada, M. (1999). Parasitoids as model organisms for ecologists. *Researches on Population Ecology*, **41**, 3-10.

Ives, A. (1988). Aggregation and the coexistance of competitors. *Annales Zoologici Fennici*, **25**, 75-88.

Krivan, V. & Sirot, E. (2004). Do short-term behavioural responses of consumers in tri-trophic food chains persist at the population time-scale? *Evolutionary Ecology Research*, **6**, 1063-1081.

McIntosh, A. & Townsend, C. (1996). Interactions between fish, grazing invertebrates and algae in a New Zealand stream: A trophic cascade mediated by fish induced changes to grazer behaviour? *Oecologia*, **108**, 174-181.

Messina, F. (1981). Plant protection as a consequence of an ant-membracid mutualism - interactions on goldenrod (Solidago sp.). *Ecology*, **62**, 1433-1440.

Nikolakakis, N., Margaritopoulos, J. &Tsitsipis, J. (2003). Performance of *Myzuspersicae* (Hemiptera:Aphididae) clones on different host-plants and their host preference. *Bulletin of Entomological Research*, **93**, 235-242.

O'Brien, R.G. & Kaiser, M.K. (1985). MANOVA method for analyzing repeated measures designs: An extensive primer. *Psychological Bulletin, 97*, 316-333.

Oksanen, L., Fretwell, S., Arruda , J. &Niemela , P. (1981). Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240-261.

Okuyama, T. &Bolker, B. (2007). On quantitative measures of indirect interactions. *Ecology Letters*, **10**, 264-271.

Pace, M., Cole, J., Carpenter, S. & Kitchell, J. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483-488.

Peacor, S. (2003). Phenotypic modifications to conspecific density arising from predation risk assessment. *Oikos*, **100**, 409-415.

Peckarsky, B. & McIntosh, A. (1998). Fitness and community consequences of avoiding multiple predators. *Oecologia*, **113**, 565-576.

Preisser, E., Bolnick, D. & Benard, M. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501-509.

Rohlfs, M. & Hoffmeister, T. (2004). Are there genetically controlled habitat-specific differences in spatial aggregation of drosophilids? *Population Ecology*, **46**, 269-274.

Roitberg, B. & Myers, J. (1978). Effect of adult Coccinellidae on the spread of plant-virus by an aphid. *Journal of Applied Ecology*, **15**, 775-779.

Rosenzweig, M. (1973). Expoitation in 3 trophic levels. *American Naturalist*, **107**, 275-294.

Schmitz, O. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science*, **319**, 952-954.

Schmitz, O., Krivan, V. & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, **7**, 153-163.

Schmitz, O. & Suttle, K. (2001). Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, **82**, 2072-2081.

Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist*, **139**, 1052-1069.

Sih, A., Englund, G. & Wooster, D. (1998).Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350-355.

Smyrnioudis, I., Harrington, R., Clark, S. &Katis, N. (2001). The effect of natural enemies on the spread of barley yellow dwarf virus (BYDV) by *Rhopalosiphumpadi* (Hemiptera:Aphididae). *Bulletin of Entomological Research*, **91**, 301-306.

Straub, C. & Snyder, W. (2006). Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology*, **87**, 277-282.

Takada, H. (2002). Parasitoids (Hymenoptera :Braconidae, Aphidiinae; Aphelinidae) of four principal pest aphids (Homoptera:Aphididae) on greenhouse vegetable crops in Japan. *Applied Entomology and Zoology*, **37**, 237-249.

Werner, E. & Peacor, S. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083-1100.