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From Individuals To Communities: The Effect Of Climate Change On Ectothermic Predators

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A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Biology

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Abstract

The living components of ecological systems exist within a nested hierarchy, consisting of individuals, populations, and communities. Because of this nestedness, climate change can greatly impact ecological systems, as whole-organism metabolic and physiological demands change for ectotherms under warming, the effects of which may compound with every succeeding level. Therefore, a multi-level approach can better isolate how climate change will reshape ecological systems. In my doctoral research, I used feeding and mesocosm experiments to examine how climate change affects ectothermic predators at the individual-, population-, and community-level, using mesostigmatic mites (Arachnida: Parasitiformes) as my model predator. My research objectives were to: 1) determine how climate warming affects predator feeding rate and behaviour, 2) test how temperature variability across two temperature ranges impacts predator populations and predator-prey interactions, and 3) identify how short-term intensive warming affects the assemblage composition of mesostigmatic mites from boreal forest soils. In my feeding experiments, I found that the predator mite *Stratiolaelaps scimitus* increasingly fed on small-bodied but not large-bodied prey under warming, which lowered their estimated energy intake. I hypothesize predators prioritized lower handling costs, rather than maximize energy gain to offset higher metabolic demands. Furthermore, I found that greater exposure of predators (and prey) populations to warmer temperatures (20 °C+) strengthened predator-prey interactions but most notably, predators consistently increased the average size of prey within their populations when exposed to warmer temperatures. Finally, I observed that short-term intensive warming shifted soil Mesostigmata assemblages, which was primarily due to the increased abundance of a single asexual species, *Veigaia mitis*. Increased abundances of asexual species under warming have not been previously reported for microarthropod predators. Across my experiments, body size, of either predators or prey, factored into how temperature increase affected ectothermic predators and predator-prey interactions. This underlines the significance of individual size in ectothermic predator-prey dynamics, but more broadly, that alterations to ecosystem-level functions may be attributed, either directly or indirectly, to changing body size distribution. Future research should further examine the relationship

between ectothermic predator and prey body size and ecosystem functions to understand how climate change will affect ecological communities.

Keywords

Climate change, ecological systems, ectotherms, Mesostigmata, microarthropods, mites, nematodes, predators, prey, temperature variability, warming

Summary for Lay Audience

The living components of ecological systems are organized into three hierarchical levels: individuals, populations, and communities. Individuals from a single species make up a population, and populations from various species interact with one another in communities. Climate change is increasing global temperatures, which will alter ecological ecosystems and the organisms that inhabit them, which predominantly are ectothermic. Ectotherms are defined as organisms that rely on environmental temperatures to regulate their internal body temperature, meaning metabolic and physiological rates (e.g., feeding, growth, and movement) will change under warming. In my doctoral research, I examined how climate change affect ectotherms, specifically ectothermic predators, using lab-based feeding and mesocosm experiments, with mesostigmatic mites (Arachnida: Parasitiformes) as my model predator group. Mesostigmatic mites are small, highly diverse arachnids, who are commonly found in soil habitats and are often sold as biocontrol agents. Because of their diversity, abundance, and small body size, mesostigmatic mites are fitting model organisms to address this question. At the individual-level, I found that predator mites altered their feeding rate by consuming more small-bodied prey, but not large-bodied prey, under warming. At the population-level, I found that predators lowered prey population abundances with the effect appearing stronger at higher temperatures. Furthermore, average body length and body size distribution of prey was both temperature- and predator-dependent. At the community-level, I found that mesostigmatic abundance increased greatly under warming, which was primarily due to a single species, *Veigaia mitis*. Unlike other mesostigmatic mite species, *Veigaia mitis* is asexual, meaning populations contain only females, suggesting a reproductive benefit for asexual species at higher temperatures. Together, my doctoral research shows that climate change will affect ectothermic predator feeding behaviour, predator-prey interactions, and predator community composition, and climate change will greatly reshape ecological systems at multiple ecological levels.

Co-Authorship Statement

Chapters 2, 3, and 4 in this thesis have been or will be submitted or are already published in their respective journals. Below I list each author contribution to the manuscript and outlined my role for each data chapter and the copyright agreement (if necessary) for published work.

A version of Chapter 2¹ has been accepted pending major revisions for publication in *Functional Ecology* and is co-authored with Kurtis F. Turnbull (KFT), Dr. Brent J. Sinclair (BJS), and Dr. Zoë Lindo (ZL). The experimental design was conceived based on conversations with BJS and ZL. I created the protocols and collected the data for movement rate, along with the choice and no choice feeding trials. Protocols for soluble proteins, neutral lipid content, and stop-flow respirometry were adapted from BJS published works. I collected soluble protein, neutral lipid, and stop-flow respirometry data and was assisted by KFT. I was responsible for the statistical data analysis and wrote the first draft of manuscript and received feedback and edits from KFT and BJS. ZL made significant contributions to manuscript writing and provided further feedback on data interpretation and presentation.

A version of Chapter 3² has been submitted to *Journal of Animal Ecology*, with ZL as the co-author. ZL and I conceived the experiment. I was responsible for the experiment set up and maintenance, as well as data collection and statistical analysis, and wrote the first draft of the manuscript. ZL made significant contributions to manuscript writing and provided further feedback on data interpretation and presentation.

A version of Chapter 4³ has been published in *Pedobiologia* (<https://doi.org/10.1016/j.pedobi.2021.150742>) with Dr. Tancredi Caruso (TC) and ZL as co-authors. ZL, TC, and I conceived the experiment. ZL collected the organic matter which acted as the substrate for this study. I was responsible for the experiment set up and maintenance, as well as data collection and statistical analysis, and wrote the first draft of the

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² Meehan, M.L., Lindo, Z. Mismatches in thermal performance between ectothermic predators and prey alter interaction strength and direction. *Journal of Animal Ecology*. Submitted March 15, 2022. JAE-2022-00180

³ Meehan, M.L., Caruso, T., Lindo, Z., 2021. Short-term intensive warming shifts predator communities (Parasitiformes: Mesostigmata) in boreal forest soils. *Pedobiologia* 87–88, 150742.

manuscript. ZL made significant contributions to manuscript writing and provided further feedback on data interpretation and presentation. *Pedobiologia* (through their publisher Elsevier) allows published works to be incorporated into graduate theses without penalty (<https://www.elsevier.com/about/policies/copyright/permissions>).

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List of Abbreviations

ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
BCA	Bicinchoninic Acid
CE	Cholesterol Esters
CH ₄	Methane
CO ₂	Carbon Dioxide
CT _{max}	Critical Maximum Temperature
CT _{min}	Critical Minimum Temperature
CWM	Community Weighted Mean
db-RDA	distance-based Redundancy Analysis
EtOH	Ethanol Alcohol
FFA	Free Fatty Acids
IPCC	Intergovernmental Panel on Climate Change
MANOVA	Multivariate Analysis of Variance
N ₂ O	Nitrous Oxide
NMDS	Non-metric Multidimensional Scaling
PPMR	Predator-Prey Mass Ratio
RQ	Respiratory Quotient
SSI	Sable Systems International
TAG	Triacylglycerols
TLC-FID	Thin Layer Chromatography-Flame Ionization Detection
T _{opt}	Optimal Temperature
TPC	Thermal Performance Curve
$\dot{V}CO_2$	Rate of Carbon Dioxide Production
$\dot{V}O_2$	Rate of Oxygen Consumption

Chapter 1

1 General Introduction

1.1 Predators in nature

Food webs consist of the feeding relationships and interactions of tens to hundreds of species or species-groups (D'Alelio et al., 2016; Kortsch et al., 2015; Morton et al., 2021) with predators sitting atop and occupying the highest positions. Predators are individuals that capture, kill and feed on other species, i.e., their prey (Sergio et al., 2014). Predators within food webs may consist of individuals and populations from a handful of species (Power, 1990), to dozens, like in soil food webs (Potapov et al., 2021, 2019). Although obscure at times, food webs can be compartmentalized into separate trophic (feeding) chains with predators often feeding on prey across multiple trophic chains and levels, thereby linking them together as energy flows upward (McCann and Rooney, 2009; Rooney et al., 2006). As such, predators can structure entire ecosystems via the consumption of their prey as predators accumulate the feeding interactions within ecosystems and regulate the flow of energy and nutrients throughout the surrounding environment (Lindeman, 1942).

Predators are integral to ecosystem function as individuals exert 'top-down' pressure on their prey, thereby reducing prey populations and releasing trophic levels below their prey from potential predation or herbivory (Hairston et al., 1960; Slobodkin et al., 1967). Top-down trophic cascades (i.e., indirect trophic effects observed beyond one trophic level) have been found in aquatic (Halaj and Wise, 2001) and terrestrial systems (Schmitz et al., 2000) and with both the addition (Ripple et al., 2001) or loss (Terborgh et al., 2001) of top predators. Although trophic cascades are typically associated with mammals, like wolves or otters (Estes and Palmisano, 1974; Ripple et al., 2001), ectothermic predators also induce cascades (Borer et al., 2005; Shurin et al., 2002), and in general, ectothermic predators are considerably more abundant and diverse than their endothermic counterparts.

Along with diet, many other attributes separate predators from their prey. The vast majority of predators are larger than their prey (Brose et al., 2019, 2006). This has

important ramifications as body size is linked to several demographic characteristics, such as population growth and density (Brown et al., 2004), and individual metabolic rate (Kleiber, 1932). Because predators are large-bodied, they have greater metabolic demands, but slower population growth and smaller populations, relative to their prey. Consequentially, it is these traits that make predators highly susceptible to environmental change (Bender et al., 2013; Cardillo, 2003; Purvis et al., 2000). For instance, reduction of habitat negatively affects large species who have larger resource bases (Cardillo, 2003); species with slow population growth take longer to recover post disturbance (Barntouse, 2004); while species with small population sizes are affected most by stochastic events (Lacy, 2000). As a result, predators are considered disproportionately sensitive to environmental change.

1.2 Climate change

Climate change is among the most prevalent forces shaping the natural world as global temperatures have increased at an unprecedented rate. Prior to the 20th century, temperatures were stable and were actually decreasing at a rate of -0.15 °C per 1000 years (PAGES 2k Consortium, 2019). But beginning in the industrial revolution (around the 1750s), greenhouse gas emissions, such as carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O), have steadily increased (IPCC, 2021) which has corresponded with a rise in global temperatures. A recent report from the Intergovernmental Panel on Climate Change (IPCC) concluded that the average global surface temperature between 2011-2020 was 1.09 [0.95 to 1.20; 90% confidence interval] °C higher than in 1850-1900, with temperature increases greatest on land compared to the ocean (land: +1.59 [1.34 to 1.83] °C, ocean: +0.88 [0.68 to 1.01] °C) (IPCC, 2021). On land, the distribution of warming is also unequal, as temperatures have increased most at high latitudes (Cohen et al., 2014), with future warming predicted to be 2-3× greater in the Arctic than the global average (Jiang et al., 2016).

Along with rising average temperatures, climate change is increasing temperature variability, as extreme warming events, like heat waves, are becoming more intense, frequent, and prolonged (Meehl and Tebaldi, 2004; Perkins-Kirkpatrick and Gibson, 2017). Already, extended heat waves have transpired as Siberia experienced

temperatures (+ 6 °C) well above the historical average for several months in 2020 (Overland and Wang, 2021). Much like average temperatures, the intensity of heat waves also varies latitudinally as the additional warmth during a heat wave, per heat wave day, is 2 – 3 °C at northern latitudes, but only 0.5 – 1 °C in the Tropics (Perkins-Kirkpatrick and Lewis, 2020). Although heat wave duration is predicted to increase most at the tropics (Perkins-Kirkpatrick and Gibson, 2017) the increasing frequency and duration of heat waves means most future boreal and austral summers may occur under heat wave conditions. Spells of high winter temperatures have also increased in recent years, as temperature records have continually been eclipsed during the winter months (Colucci et al., 2017; Hansen et al., 2014).

One the most concerning issues with climate change is not the magnitude of warming, but rather the rate of warming. Diffenbaugh and Field (2013) found that the projected rate of temperature change could be at least 10× and upward of 100× faster than observed in the past 65 million years. Organisms today are living within climates that are dissimilar to even their most recent ancestors. To this end, climate change has already reshaped the natural world and its ecological communities. Commonly, this includes changes to species distribution (where species inhabit) (Parmesan and Yohe, 2003; Román-Palacios and Wiens, 2020), species phenology (the timing of life history events) (Montgomery et al., 2020; Scranton and Amarasekare, 2017), and to individual body size (Gardner et al., 2011). Due to the close ties between environmental temperatures and biological rates for ectotherms, ectotherms are particularly susceptible to climate change.

1.3 Ectotherms, ectothermic predators and climate change

To comprehend how climate change can reshape the natural world, one needs to understand how virtually all organisms respond to warmer (or cooler) temperatures. More than 99% of species are ectotherms (Atkinson and Sibly, 1997) and the majority of animal biomass is concentrated within ectothermic animals, like arthropods (Bar-On et al., 2018). Unlike endotherms, ectotherms do not generate metabolic heat to regulate their body temperature, meaning environmental temperature sets their pace of life as metabolic and physiological rates (e.g., feeding, growth, and movement) are tightly coupled to one another (Clarke, 2017).

Whole-organism metabolic and physiological rates (grouped here as ‘performance’) follows a well-established relationship with temperature and can be shown using a thermal performance curve (TPC) (Sinclair et al., 2016) (Figure 1-1). The width (i.e., the thermal breadth) of TPCs are bounded by the minimum (CT_{min}) and maximum (CT_{max}), i.e., the temperature limits when performance happens. TPCs are typically skewed as ectotherm performance starts at CT_{min} and increases curvilinearly quickly before slowing down when approaching the thermal optimum (T_{opt}). Here, performance is maximized as temperatures beyond this leads to declining performance with performance ceasing at CT_{max} . The overall shape of the curve can be performance- (Stevenson et al., 1985) and species-specific (Rezende and Bozinovic, 2019) as the temperature-performance relationship is highly variable.

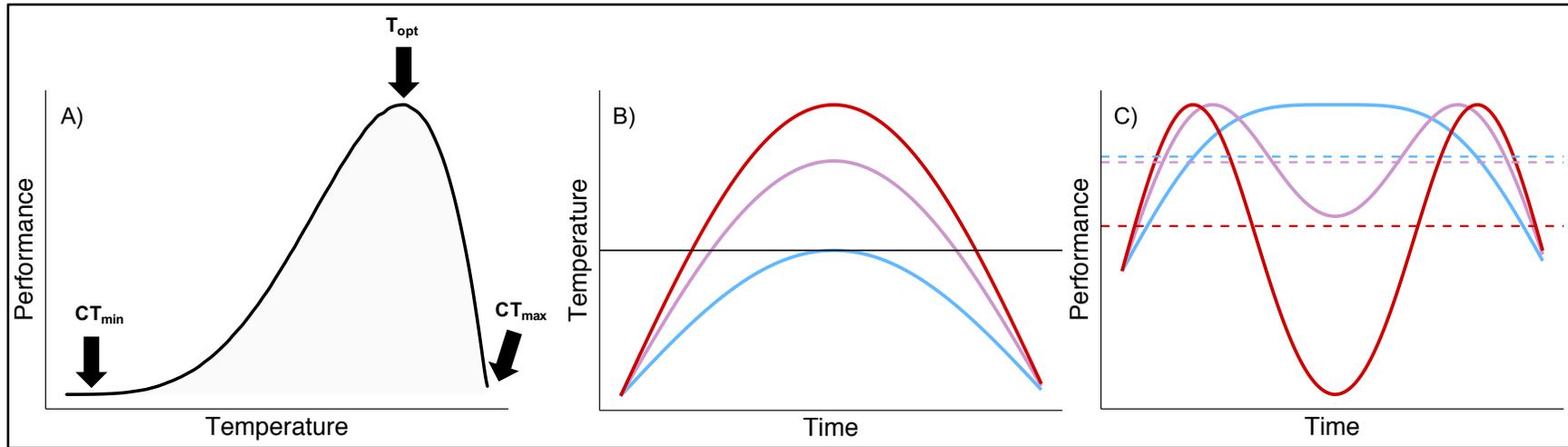


Figure 1-1 A conceptual thermal performance curve showing the temperature – performance (e.g., whole-organism metabolic and physiological rates) relationship for an ectotherm.

A) Ectotherm performance is bounded by critical minimum (CT_{min}) and critical maximum (CT_{max}) temperatures as performance is highest (or maximized) at the thermal optimum (T_{opt}). Warming below T_{opt} corresponds with higher performance, but if warming continues beyond T_{opt} then performance declines. B) Three hypothetical temperature cycles where temperatures rise then falls to varying degrees. The horizontal line corresponds with T_{opt} used to model performance in Figure C. C) Corresponding ectotherm performance under three different temperature cycles. Ectotherm performance was based on the equation (and parameters) for consumption rate of Silver Carp (*Hypophthalmichthys molitrix*) provided in Cooke and Hill (2010). Dotted horizontal lines represent the average performance for the three temperature cycles. This conceptual figure was modeled after Figures in Colinet et al. (2015) and Sinclair et al. (2016).

The average performance for an ectotherm differs under constant vs. fluctuating temperatures, due to the curvilinear relationship between temperature and performance. This relationship can be described using a mathematical property of non-linear functions called Jensen's inequality (Jensen, 1906; Ruel and Ayres, 1999). Jensen's inequality states that when variance is greater than zero, the average value at $f(x)$ does not equal the result of \bar{x} at $f(\bar{x})$, with the difference in performance dependent on whether the second derivative is positive or negative. In simpler terms, average performance is higher under fluctuating temperatures when temperatures remain below T_{opt} , but are lower when temperatures fluctuate above T_{opt} (Colinet et al., 2015; Figure 1-1). This difference in performance between constant and fluctuating temperatures is further exacerbated when individuals (and their specific functions) are temperature sensitive and temperature cycles exhibit large amplitudes. Because of this, recent publications have stressed incorporating temperature variability into studies to better predict how climate change will impact ectotherms (Bernhardt et al., 2019; Kingsolver et al., 2015; Marshall et al., 2021; Morash et al., 2018).

Climate change may impact ectothermic predators through direct (changing metabolic and physiological demands) and indirect (changing prey resources and competition) mechanisms. Initial research indicates that ectothermic predators are disproportionately sensitive to warming, relative to their prey, as shown through mathematical models (Vasseur and McCann, 2005), microcosm experiments (Petchey et al., 1999), and correlative analyses (Voigt et al., 2003). And while more recent studies have provided further evidence to support this claim (e.g., Edeline et al., 2013; Fussmann et al., 2014), the susceptibility of ectothermic predators to climate change is likely far more complex as numerous factors dictate ectothermic predator success at higher temperatures. For instance, nutrient (carbon and nitrogen) demands (Bestion et al., 2019; Zhang et al., 2020), prey community composition (Yvon-Durocher et al., 2015, 2011), predator and prey encounter/movement rates (Kruse et al., 2008; Öhlund et al., 2014), tolerance to extreme temperatures (de Mira-Mendes et al., 2019; Franken et al., 2018; Pintanel et al., 2021), amongst other factors affect predator persistence under warming. Therefore, to isolate how rising temperatures from climate changes affects ectothermic

predators requires the examination of predator group(s) across multiple ecological levels to better assess the effects of warming across each succeeding level.

Increasing mean, variability or both mean and variability of temperature with climate change will impact individual-level functions for ectothermic predators, the effects of which may compound within higher ecological levels (i.e., predator and prey populations and communities) (Figure 1-2). For example, warming (below T_{opt}) increases ectotherm feeding and attack rates (Rall et al., 2012), which can lead to greater interaction strength (i.e., the effect of one species on the abundance or biomass of another; Berlow et al., 1999) between consumers and resources (O'Connor, 2009; Rall et al., 2010). Higher feeding rates by predators paired with changing prey preference may shift prey community composition; Yvon-Durocher et al. (2015) found that community composition of phytoplankton shifted towards being larger and more heavily defended, as zooplankton presumably fed more on smaller-bodied phytoplankton under warming. Finally, higher feeding rates by top predators may restructure food webs by shifting the regulation of primary production from bottom-up forces to top-down ones (Kratina et al., 2012; Shurin et al., 2012). Together, this suggests that even slight changes to temperature can have cascading effects for whole ecosystems and food webs. But the challenge of understanding the effect of climate change on ectothermic predators is not only in examining how warming alters predator functions, predator-prey interactions, and predator communities, but also identifying potential mechanisms that explain these changes and finding common trends and patterns across ecological levels. This is particularly challenging in highly diverse food webs, like soil food webs, where predators can consist of multiple taxonomic groups with various diets and rates, meaning climate change may greatly disrupt these communities as predator and prey alike adjust to new conditions.

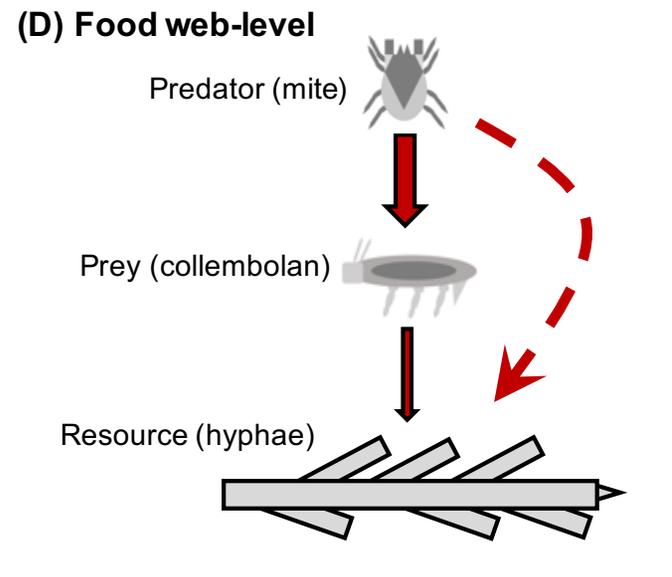
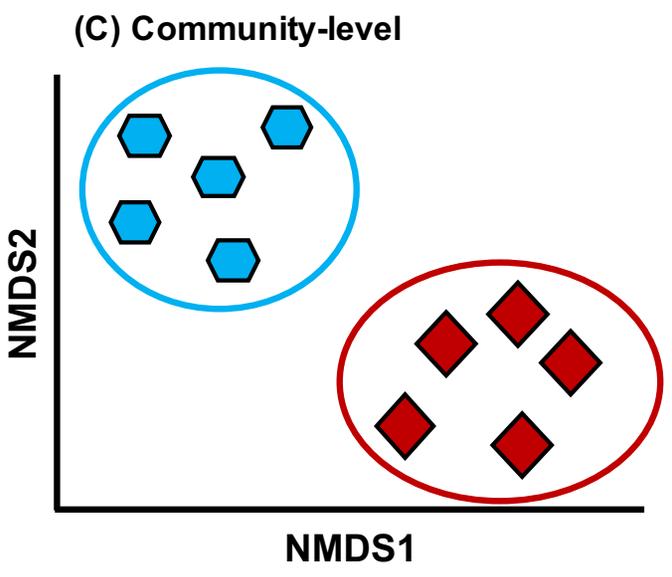
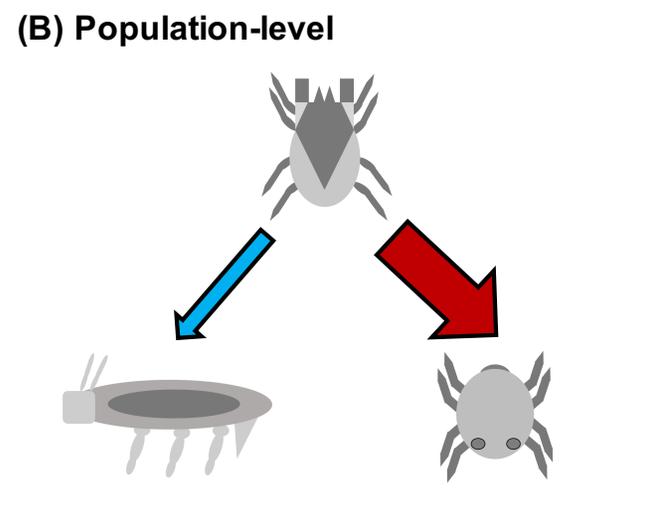
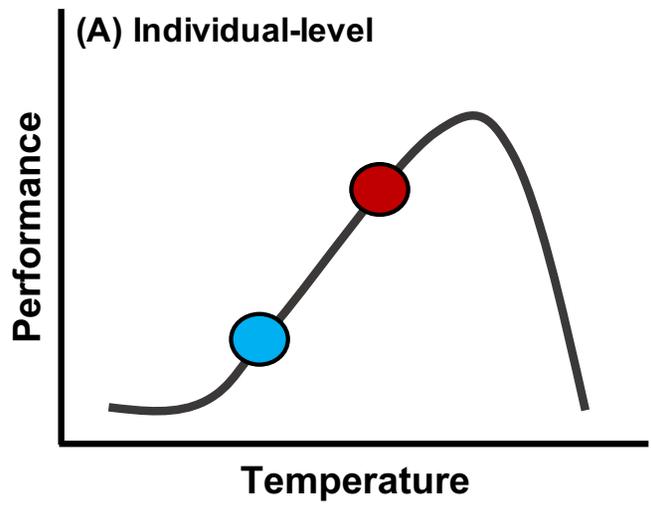


Figure 1-2 A conceptual figure showing some examples of how climate change can affect ectothermic predators and predator-prey interactions across multiple ecological levels.

Warming increases ectothermic performance, like feeding rates (Figure A), paired with changing feeding behaviour can lead to greater predator-prey interaction strength for select prey (Figure B) and shift prey community composition (as illustrated with a non-metric multidimensional scaling (NMDS) plot; Figure C). These interactions accumulate within food webs where the balance can shift towards top-down forces (Figure D). Conceptual figures are shown using microarthropod animals, consisting of predator and prey mites, and collembolan prey, and soil fungi. Here, arrows represent feeding relationships, while the size of arrows (in Figures B and D) represent the strength of those relationships. In Figure D, solid arrows represent direct interactions, while the dotted arrow is an indirect interaction. Blue represents functions, interactions, and community compositions under cooler temperatures, while red represents them under warmer temperatures.

1.4 Mesostigmatic mites (Arachnida: Parasitiformes: Mesostigmata)

Soil food webs are highly diverse as several microbial and animal groups interact with one another across multiple trophic (feeding) levels (Hunt et al., 1987; Moore et al., 2003). These food webs are mainly populated by microarthropods, like mites (Arachnida: Acariformes, Parasitiformes) and collembolans (Hexapoda: Collembola), along with nematodes (Nematoda), and microbes (fungi, bacteria and protists) forming the basal consumer levels) (Coleman et al., 2018). Mites, collembolans, and nematodes primarily function as fungi- and detritus-feeding in soil food webs, but soil microarthropod predators sit atop of the soil food web, which at times, can consist of entirely of one group, mesostigmatic mites.

Mesostigmata are a speciose group of arachnids with 11,000 described species, of which 650 species have been found in Canada thus far (Beaulieu et al., 2019; Walter and Proctor, 2013). Mesostigmatic mites can be found in anthills or animal nests (Napierała and Błoszyk, 2013), on living plants (McMurtry et al., 2013; McMurtry and Croft, 1997), while some species are bee parasites (Ramsey et al., 2019), or reared commercially as biological control agents (Knapp et al., 2018). However, most mesostigmatic mites are soil-dwelling, where their abundances can exceed 10,000 individuals per m² (Christian, 2000). Despite being one magnitude smaller than other soil predators, soil mesostigmatic mites total biomass can match or exceed that of spiders and beetles (Scheu et al., 2003) due to the immense number of individuals within their communities.

The Mesostigmata life cycle has three juvenile stages: larva, protonymph, deutonymph, before moulting into adults (Lindquist et al., 2009). Body size increases with ontogeny as individual body length can range between 200 – 4,500 µm (Lindquist et al., 2009), with an adult body mass for most species between 2 – 60 µg (Newton and Proctor, 2013). Despite mesostigmatic species having the same number of developmental stages, mesostigmatic mites exhibit numerous types of sexual systems. Many species are biparental, with males and females reproducing sexually, leading to equal male : female ratios within populations (Norton et al., 1993). However, parthenogenesis (asexual reproduction) is common within Mesostigmata. For

Mesostigmata, arrhenotokous parthenogenesis arises when males are produced asexually but females sexually, which can result in female-biased sex ratios within populations (Norton et al., 1993). Thelytokous parthenogenesis is also observed within Mesostigmata within a select number of families, like Ascidae and Veigaiidae and leads to all-female populations (Norton et al., 1993).

Soil Mesostigmata are considered generalist predators as individuals will consume nematodes, collembolans, and soft-bodied mites (e.g., prostigmatic mites, and juvenile oribatid and other mesostigmatic mites) (Beaulieu and Walter, 2007; Schneider and Maraun, 2009; Usher et al., 1989; Walter, 1988; Walter et al., 1988), and can feed on prey both smaller and larger than themselves (Bowman, 1987; Rahmani et al., 2016; Usher and Bowring, 1984). However, some mesostigmatic mite species are specialist feeders. An example are species within the family Zerconidae. Feeding experiments have shown zerconid species exclusively feed on nematodes (Walter, 1988) and have been used as specialist and nematode feeders within predator-prey experiments (Laakso and Setälä, 1999; Martikainen and Huhta, 1990). Differences in feeding preferences amongst mesostigmatic species may affect soil food web dynamics. Laakso and Setälä, (1999) found that nematode-feeding specialists had greater top-down control on prey populations than generalists, and significantly reduced the biomasses of both bacteria- and fungi-feeding nematodes within experimental mesocosms.

Mesostigmatic mites have been used as model predators across numerous research topics because they are small, diverse, are generalist feeders, and can be easily sampled and maintained in various climatic conditions (i.e., temperature and moisture levels). This includes studies on predator-prey interactions with respect to predator learned behaviour (Jensen et al., 2019b; Schausberger et al., 2010), predator's non-consumptive effects on prey (Walzer and Schausberger, 2009), spatial-temporal population dynamics (Huffaker, 1958; Janssen et al., 1997; Lesna et al., 1996; Nachappa et al., 2011), ecotoxicology (Axelsen et al., 1997), and predator functional response (Lester et al., 2005; Lester and Harmsen, 2002). In conjunction, because mesostigmatic mites are speciose, their assemblages, along with other soil fauna groups, can act as model systems to understand how environmental change shapes community dynamics. For example, Staddon et al. (2010) used microarthropod communities to study how habitat connectivity

affects ecosystem-level processes, such as carbon and nitrogen fluxes and found that mesostigmatic mite predators were disproportionately impacted by habitat loss, and reductions in predator mites led to prey release and changes in C and N cycling. Recently, mesostigmatic mites have been used to model predator behaviour, predator-prey dynamics, and predator physiological demands in response to temperature change (Jensen et al., 2019a, 2018, 2017; Thakur et al., 2018, 2017). Using model organisms (and simplified experimental settings) can breakdown how climate change is affecting ectothermic predators across multiple ecological levels. By examining mesostigmatic mites at the individual-, population, and community-level, I can improve our understanding of how climate change will affect ectothermic predators.

1.5 Thesis objectives

The overall objective of my thesis was to test the effect of climate change on ectothermic predators across multiple ecological levels (individual-, population, and community-level), using mesostigmatic mites as my model predator. By examining a single predator group across multiple levels, I can better isolate how warming affects ectothermic predator individuals, populations and communities. The specific research objectives of my thesis were to:

1. Determine how increasing temperatures affect the individual feeding rate and behaviour of an ectothermic predator, *Stratiolaelaps scimitus* (Chapter 2)
2. Test the interactive effect of temperature increase, variability, and predation on population-level predator-prey dynamics in a microarthropod-model system (Chapter 3)
3. Identify how short-term intensive warming affects the assemblage composition of mesostigmatic mites collected from the boreal forest (Chapter 4)

In my second chapter, I determined how temperature (16 °C vs. 24 °C) affected the feeding rate and behaviour of an ectothermic predator *Stratiolaelaps scimitus* (Mesostigmata: Laelapidae) using choice and no choice feeding experiments and offering predators three prey species that differed in capturability (body size, movement rates), energy content (lipid and protein content), and defenses. I measured the CO₂ production of predators to calculate their energy demands during the feeding experiment at 24 °C,

compared to 16 °C. I also quantified the energy intake of predators in the choice feeding experiments to determine if energy intake increased or decreased at 24 °C compared to 16 °C.

In my third chapter, I determined how increasing mean and temperature variability affect predator-prey dynamics across a cool (12 °C to 20 °C) and warm (20 °C to 26 °C) temperature range using a model predator (*Stratiolaelaps scimitus*) and prey (*Folsomia candida* (Collembola: Isotomidae)) species. To do this, I counted predator and prey abundance, measured predator and prey body length, and calculated predator-prey interaction strength and predator-prey mass ratio within experimental mesocosms.

In my fourth chapter, I incubated boreal forest, forest-floor organic matter at 12 °C and 20 °C for three months to determine how short-term intensive warming impacts Mesostigmata assemblages by counting mesostigmatic mite juveniles and identifying adults to the species-level. In addition, I enumerated the abundances of oribatid, astigmatic, and prostigmatic mites, along with collembolans and nematodes, to determine if prey abundances affected mesostigmatic mite assemblages. I tested this by using a mixture of both community- (species richness, abundance, diversity, evenness, and assemblage composition) and trait-based indices (community weighted mean of mesostigmatic body mass).

In my fifth and final chapter, I synthesize my research by establishing connections between my three data chapters and discussing the broader implications of my results.

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Chapter 2

2 Predators minimize energy costs, rather than maximize energy gains under warming: Evidence from a microcosm feeding experiment

2.1 Introduction

Predators exert energy searching for, capturing, and handling their prey. Optimal foraging theory predicts that predators should select and prefer prey that maximizes energy intake while balancing the energetic costs associated with prey capture and handling, alongside digestion and metabolism (Stephens and Krebs 1986; Stephens et al. 2007). Specifically, predators may select prey according to their nitrogen:carbon ratio (Jensen et al., 2012), energy density (Kiyota et al., 2013), body size (Johnson et al., 2012) and defenses (Llewelyn et al., 2012). However, these prey characteristics are not necessarily independent of one another. For instance, body size influences prey movement rate, which in turn affects capturability and handling time (Brose et al., 2008; Hirt et al., 2017), suggesting that prey body size strongly factors into predator foraging decisions and outcomes.

Increased temperatures from climate change is affecting predator-prey dynamics as warming increases ectotherm metabolic rates, altering the balance between energetic costs and energetic gains (Rall et al., 2010; Vucic-Pestic et al., 2011). Warming will also change both predator and prey movement rates (Kruse et al., 2008) and nutrient demands (Bestion et al., 2019) altering predator-prey interactions under higher temperatures. Acclimation to warming may buffer against rising metabolic demands (Sentis et al., 2015; Sohlström et al., 2021), but predators can also compensate by increasing their overall feeding rate (Ramachandran et al., 2021; Walker et al., 2020), or prioritizing prey that are easier to subdue and capture. For example, Frances and McCauley (2018) found that intraguild predation of dragonfly larvae under warming shifted the body size distribution towards larger-bodied individuals of three species, as individuals increasingly fed on smaller-bodied ones. Possibly, this occurred because smaller animals typically

have slower movement rates than larger animals (Alexander, 1982; Peters, 1983), while smaller-bodied prey lower handling times for predators (Brose et al., 2008; Rall et al., 2012), making them less energetically costly to capture and feed on. However, because smaller prey are less energy-rich than larger prey (Portalier et al., 2019), predators need to consume more small-bodied prey to satisfy their energetic demands. But on top of this, predators need to balance carbon (to fuel metabolism) and nitrogen (for growth and maintenance) demands (Angilletta Jr., 2009; Bestion et al., 2019; Lee et al., 2015; Lemoine et al., 2013) that are also impacted by prey body size as large-bodied prey inherently have more carbon- and nitrogen-rich tissue than small-bodied prey. Thus, climate change produces trade-offs for ectothermic predators between consuming easier to capture, small-bodied prey, with difficult to capture large-bodied prey but with greater energy and nutrient content.

Warming-induced shifts in predator feeding behaviour and prey preference may affect multiple trophic levels. For instance, if ectothermic predators increase their feeding rates under warming, then top-down control by predators will strengthen (Kratina et al., 2012; Shurin et al., 2012) that can produce trophic cascades towards basal resources (Lang et al., 2014). Changing predator feeding behaviour may also have unexpected predator-prey outcomes that affect other ecosystem-level processes. For example, Koltz et al. (2018) found that collembolan abundance increased with wolf spider (*Lycosidae* spp.) density under warming in the Arctic tundra, which they theorized was due to changes in predator feeding rate and behaviour. These changes corresponded with slower decomposition rates as greater abundances of collembolans likely suppressed fungal biomass, one of the main decomposers in belowground systems. Thus, developing a better understanding of how predators alter their feeding behaviour under warming is key to predicting changes to overall food web structure and interactions.

In this study I examined how an ectothermic predator alters its feeding behavior to compensate for increased metabolic demands under warming by conducting choice and no choice feeding trials and offering predators three prey species that differed in capturability, energy content, and defenses. Predators should select for prey based on trade-offs due to the energetic gains versus losses related to handling and consumption. I hypothesize three possible outcomes in my feeding trials. First, predators will increase

their overall feeding rate to compensate for the increased metabolic demands, thus the survival rate during predation of all three prey species will decrease with increasing temperature. Second, predators will minimize the cost of feeding (i.e., the energy spent capturing and handling prey) under warming. In this case, I predict predators to feed more on small-bodied prey under warming because they are easier to capture and consume. Third, predators will maximize energy intake under warming, and I predict that predators would feed more on large-bodied prey under warming.

2.2 Methods and Materials

2.2.1 Predator and prey species

I used the predatory mite *Stratiolaelaps scimitus* (Arachnida: Mesostigmata: Laelapidae) and three prey species in my experiment: one collembolan, *Folsomia candida* (Hexapoda: Collembola: Isotomidae), and two mites: *Oppia nitens* (Arachnida: Oribatida: Oppiidae) and *Carpoglyphus lactis* (Arachnida: Astigmata: Carpglyphidae). *Stratiolaelaps scimitus* is a medium-sized (600 – 700 μm in length) active, generalist soil predator that feeds on a wide variety of soil invertebrates, including dipteran larvae, potworms, soft-bodied mites, insect eggs, and can even ingest pollen (Cabrera et al., 2005; Xie et al., 2018). *Stratiolaelaps scimitus* are consistently on the move, searching for prey, and like other mesostigmatic mites, feed using a piercing-sucking extra-oral digestion mode as individuals will pre-orally digest their prey before consumption (Cohen, 1995).

The prey I used differ in body size, shape, as well as defensive traits. *Folsomia candida* is a large (adult body length can exceed 1500 μm) (Fountain and Hopkin, 2005) soil animal but is readily consumed by mesostigmatic mite predators (Jensen et al., 2019; Thakur et al., 2017). Like many Collembola, *F. candida* can escape predators by jumping using its furcula (Fountain and Hopkin, 2005). *Oppia nitens* is a well-sclerotized, medium-sized soil mite (body length $\sim 510 \mu\text{m}$) (Fajana et al., 2019). Because of this sclerotization, adult oribatid mites, like *O. nitens*, are well-defended and not often consumed by soil mesostigmatic mites (Peschel et al., 2006). However, *O. nitens* were included as ectothermic predators may feed more on less susceptible prey when under higher metabolic demands from climate warming. *Carpoglyphus lactis* is a

small (body length ~300 µm) soft-bodied astigmatid mite that has no known defenses (Zhan et al., 2017). Although not found in soil, *C. lactis* is similar in shape and size with soft-bodied juvenile oribatid mites, who are a common prey group for soil mesostigmatic mites (Schneider and Maraun, 2009).

I maintained cultures of *F. candida* and *O. nitens* from Environment and Climate Change Canada (Ottawa, ON) on a dry yeast (Active Dry Yeast, Fleischmann's Instant Yeast, Lasalle, QC, Canada) diet in sterilized soil. I purchased and maintained cultures of *C. lactis* from Koppert Canada Limited (Toronto, ON, Canada) on dry wheat bran spiked with small pieces of dried apricot. I also purchased *S. scimitus* from Koppert Canada Limited; they were shipped with *Tyrophagus putrescentiae* as prey, which was exhausted seven days after arrival. Thereafter, I maintained *S. scimitus* cultures on *C. lactis* for the duration of the experiment. Because >95% of individuals in my *S. scimitus* cultures were female, I only used adult females in my feeding trials. I maintained cultures of my animals in plastic food storage containers (e.g., Tupperware, Ziploc). I added food and moistened culture media once per week for *F. candida* and *O. nitens* cultures, and twice per week for *S. scimitus*. I moistened *C. lactis* cultures at the start but did not water cultures again to limit potential mold growth on bran, while the dried apricot offered at the beginning of culturing supplemented their diet for the entire experiment.

I kept predator and prey cultures in B.O.D Low Temperature Incubators (VWR Model 2005; Plainfield, NJ, USA) at 16 °C or 24 °C (± 0.5 °C) with 60 – 90% relative humidity in constant darkness for at least one full generation (five weeks for *F. candida*, *O. nitens*, and *S. scimitus*, and three weeks for *C. lactis*), before moving them to a GCHA-10 Environmental Growth Chamber (Chagrin Falls, OH, USA) at 16 °C or 24 °C (± 0.5 °C) with 40 – 70% relative humidity in constant darkness one week prior to my experiment. Switching from incubators to the growth chamber allowed me to measure movement rate and conduct the feeding trials within the same apparatus.

2.2.2 Stop-flow respirometry

I used stop-flow respirometry to measure CO₂ production at 12 °C, 16 °C, 20 °C, 24 °C, and 28 °C of *S. scimitus* individuals maintained at 16 °C or 24 °C to gauge the

metabolic demands of predator mites maintained and tested at the two temperatures in my experiment (Smith et al., 2021). I only included data for 16 °C-maintained *S. scimitus* measured at 16 °C, and 24 °C-maintained *S. scimitus* measured at 24 °C as those were the experimental conditions used in the feeding trials; but the entire temperature-CO₂ relationship is presented in Appendix A, Figure 1A. I measured the CO₂ production of groups of 25 adult female *S. scimitus*, with four replicates at each temperature.

Stratiolaelaps scimitus were held in chambers that consisted of c. 3 cm lengths of Bev-A-Line V tubing (Cole-Parmer; Vernon Hills, IL, USA) inside of a Peltier temperature-controlled cabinet (PELT-4; Sable Systems International (SSI); Las Vegas, NV, USA). I equilibrated each group of animals for 30 min at each test temperature, and sequentially flushed each chamber with dry, CO₂-free air for 10 min. I included a blank chamber when measuring CO₂ production to act as a control for my four experimental chambers and used an RM8 multiplexor (SSI) to manage air flow. I allowed *S. scimitus* to respire in the chambers for 230 minutes where the air was then passed through a LiCor Li7000 infrared gas analyzer (Lincoln, NE, USA) at 200 mL min⁻¹ against a baseline stream of dry, CO₂-free air to measure the volume of accumulated CO₂. I collected data in Expedata software (ver. 1.8.5.; SSI) via a UI2 interface (SSI) and estimated rate of CO₂ production ($\dot{V}\text{CO}_2$) by dividing the volume of CO₂ produced by the duration the chamber was sealed.

I converted $\dot{V}\text{CO}_2$ to estimated energy demands during the feeding trials for *S. scimitus* individuals (mJ 8 h⁻¹ individual⁻¹) to gauge energy lost through respiration versus the energy intake by predators when feeding. Briefly, I converted $\dot{V}\text{CO}_2$ into $\dot{V}\text{O}_2$ by dividing $\dot{V}\text{CO}_2$ by an assumed respiratory quotient (RQ) of 0.8 (Lighton, 2008). I then multiplied $\dot{V}\text{O}_2$ by the oxyjoule equivalent (20.13 J mL⁻¹) to calculate metabolic rate (J s⁻¹), which I then converted to estimate energy demands during the feeding trials (mJ 8 h⁻¹ individual⁻¹; see Appendix A, *Energy demands of Stratiolaelaps scimitus* individuals for more details).

2.2.3 Neutral lipid and soluble protein measurements

I measured the total neutral lipids and soluble protein of all taxa (*C. lactis*, *F. candida*, *O. nitens*, and *S. scimitus*) after acclimation to 16 °C or 24 °C using methods

adapted from Williams et al. (2012) to estimate the energy content ($\text{mJ individual}^{-1}$) of both predators and prey. For each species, I pooled individuals into samples of 0.3 – 2.5 mg wet mass, which included both adult and juveniles of *C. lactis*, and *F. candida*, and adults of *O. nitens* and *S. scimitus*. For total neutral lipids, I homogenized tissue and extracted lipids in 2.5 mL of Folch reagent [2:1 chloroform: methanol (v:v) mixture containing 0.1 % butylated hydroxytoluene (w/v, BHT)]. I did not detect cholesterol during preliminary analyses, so I added 100 μL of 1 mg mL^{-1} cholesterol in chloroform (Sigma-Aldrich; St. Louis, MO, USA) to every sample as an internal standard to correct for lipid lost during extraction. I vortexed and centrifuged samples ($2000 \times g$ for 15 min), then added 1 mL of 0.25% KCl to each sample before incubating at 70 °C for 10 min. After incubation, I collected the organic phase, containing the neutral lipids, and dried it under a stream of nitrogen gas. Samples were then reconstituted in 100 μL of Folch reagent and stored at -20 °C until analysis.

I dried samples again before reconstituting lipid samples in 50 μL chloroform. I separated neutral lipid classes in triplicate on chromarods (Shell-USA; Spotsylvania, VA, USA) in a development tank of 49:21:0.35 benzene: chloroform: formic acid for 45 min. I used a known standard mixture to identify classes of neutral lipids in my samples by comparing the retention time of individual peaks (Williams et al., 2011). I measured the cholesterol esters (CEs), triacylglycerols (TAGs), and non-esterified ‘free’ fatty acids (FFAs), as I detected them in my samples, using three standard curves [Triarchin (TCI; Tokyo, Japan), triplamitin (Sigma-Aldrich) and triolein (Sigma-Aldrich) mixed equally into a TAG standard; cholesterol palmitate (Sigma-Aldrich) as a CE standard; and stearic and palmitic acid (Sigma-Aldrich) mixed equally into a FFA standard]. I quantified these lipids using an Iatroscan MK-6 TLC-FID (thin layer chromatography-flame ionization detection) at a scanning speed of 3 cm s^{-1} and flow rates of 2 L min^{-1} air and 160 mL min^{-1} hydrogen and normalized each value to my cholesterol internal standard. I had three biological replicates for each taxon at each temperature but discarded one replicate of *O. nitens* at 24 °C because FFAs were not detected in the sample.

I used a bicinchoninic acid (BCA) assay (Thermo Fisher Scientific; Williams et al., 2012) to quantify total soluble protein content of each taxon. I homogenized groups of animals in 40 μL 0.05% Tween-20 before centrifuging ($600 \times g$, 5 min), and diluting 5

μL of supernatant in 40 μL 0.05% Tween-20. I added 200 μL of BCA reagent [50:1 bicinchoninic acid: 4% copper(II) sulphate w/w in water] and incubated overnight at room temperature ($\sim 21\text{ }^{\circ}\text{C}$). I read absorbance at 562 nm and compared the values to a bovine serum albumin standard (Sigma-Aldrich; 0.025 mg mL^{-1} - 2 mg mL^{-1} in 0.05% Tween-20). For total soluble protein content, I had three technical replicates for each of my three biological replicates for each taxon at each temperature.

Finally, I used average soluble protein and lipid concentration (total $\text{mg mg of sample}^{-1}$) values at each temperature (16 $^{\circ}\text{C}$ and 24 $^{\circ}\text{C}$) to estimate the total energy content of an average-sized individual (in $\text{mJ individual}^{-1}$) for each species. I used length-mass conversion formulae to estimate the body mass of my four species based on species description and available literature. I calculated energy content by assuming an energy density of 17.8 J mg^{-1} for soluble protein and 39.3 J mg^{-1} for lipids (Schmidt-Nielsen, 1990). For each species, I multiplied their estimated body mass by the concentration of lipids and protein with their respective energy densities to calculate their energy content at 16 $^{\circ}\text{C}$ and 24 $^{\circ}\text{C}$. For more details on how I calculated energy content of each taxa, see Appendix A, *Calculating body mass and energy content for predators and prey*.

2.2.4 Movement rate

I measured the movement rate of all four species within a given time at each acclimation temperature using protocols adapted from *Drosophila* studies (Chang et al., 2006; Simon et al., 2009) to determine the speed of predators, relative to their prey. This measurement accounted for how changing predator and prey movement rates may impact predator feeding under warming. I placed an individual animal on a printed grid (2 \times 2 mm cells) covered by a 3-D printed ring (height: 0.5 cm) with a 2 mm thick glass covering. I varied the diameter of the ring between predator (6 cm) and prey (4 cm) to accommodate the faster movement rates of the predators and give individuals more interior space to move in. I recorded the movement of individuals inside the GCHA-10 Environmental Growth Chamber using a Nikon D610 digital SLR camera paired with the AF-S Micro NIKKOR 105 mm1:2.8G ED lens with a red LED light illuminating the grid. I recorded 60 s videos to ensure at least one continuous period of 15 to 30 s of constant

movement (Appendix A; Image 1A) with a clear view of both the individual and the grid lines. I scored the total movement of predators and prey by counting the number of cell lines each individual crossed. I scored the same 15 – 30 s video clip three times and recorded the mean number of lines crossed and measured 10 – 12 replicates of total movement for each taxon at 16 °C and 24 °C.

2.2.5 Feeding assays

I conducted choice (three prey) or no choice (single prey) feeding trials for adult female *S. scimitus* in constant darkness at 16 °C or 24 °C in the GCHA-10 Environmental Growth Chamber. By conducting both choice and no choice feeding trials, I assessed whether predator mites had similar feeding rates and behaviours when in the presence of more than one prey species. To ensure predators would feed during the trials, prior to feeding trials I food deprived individual predators for three days in constant darkness in 1.5 mL microcentrifuge tubes with a moist piece of filter paper to prevent desiccation of predator mites. I used adult *O. nitens*, and a mixture of adult and juveniles for *C. lactis* and *F. candida* in feeding trials. I selected *F. candida* individuals that were the same size or larger than *S. scimitus* (> 700 µm body length), with size ranging from 700 µm and 2000 µm long.

The feeding arena consisted of a 40 mm diameter petri dish containing a solid substrate of 9:1 plaster of Paris to activated charcoal, where I added four drops of distilled water to maintain humidity in the arena. I observed feeding through a 5 × 5 cm glass covering secured to the top of the petri dish to stop animals from escaping (Appendix A; Image 2A). In the choice feeding experiment, I placed five individuals of each prey species (*C. lactis*, *F. candida*, and *O. nitens*) and one *S. scimitus* (15 prey : 1 predator) into the feeding arena for 8 h. In the no choice feeding experiment, I placed five individuals of a single prey species into an arena with a single *S. scimitus* (5 prey : 1 predator) for 8 h. I recorded the number of live prey remaining every 30 minutes to determine the survival rate of each prey species. I completed 9 – 10 choice trials and 8 – 12 no-choice trials for each prey species at each temperature.

2.2.6 Estimated energy intake

I estimated the energy intake (in mJ 8 h⁻¹ individual⁻¹) for each *S. scimitus* individual in the choice feeding trials at 16 °C and 24 °C by multiplying the feeding rate of the individual predator by the change in mass of a predator post feeding, along with the energy density of their prey and the assimilation efficiency of predators. Change in body mass for predators was by measuring the length and width of predator mites before and after feeding on *C. lactis* and *F. candida*, then converting those measurements into mass and standardized values by number of prey eaten (for more information please see Appendix A, *Estimated energy intake of Stratiolaelaps scimitus during the choice feeding experiment*). The formula to calculate energy intake is as follows:

$$I_t = \sum_j^T (F_{j,T} \times C_{j,T} \times E_{j,T}) \times Ae$$

where I = is the energy intake in 8 h by a single *S. scimitus* (mJ 8 h⁻¹ individual⁻¹) at temperature T (16 °C or 24 °C), feeding on all prey, F = feeding rate (number of prey individuals 8 h⁻¹) of *S. scimitus* at temperature T (16 °C or 24 °C) for a given prey j (*C. lactis* or *F. candida*), C = the change in body mass (µg prey eaten⁻¹) for *S. scimitus* at temperature T (16 °C or 24 °C) when feeding on prey j (*C. lactis* or *F. candida*) (Appendix A; Table 1A), E = is the energy density (mJ µg⁻¹) at temperature t (16 °C or 24 °C) for prey j (*C. lactis* or *F. candida*) (Table 2-1). The assimilation efficiency (Ae) for *S. scimitus* was assumed to be 0.85 (Jochum et al., 2017).

2.2.7 Statistical Analysis

I performed all analyses using the R statistical program (R Version 3.5.1; R Core Team 2018). For all statistical tests, I evaluated the underlying assumptions of each model. I used a one-way Analysis of Variance (ANOVA) to determine the effect of temperature (16 °C or 24 °C) on CO₂ production of *S. scimitus*. In addition, I tested for differences between species in their total soluble protein (in mg) and neutral lipid content (in mg) at 16 °C and 24 °C using Analysis of Covariance (ANCOVA). For total lipid and protein content, the fixed factors were taxon, temperature, and their interaction, with the sample mass (pooled wet mass, in mg) as the co-variate. I then summarized my model

using the ‘Anova’ function (in the *car* package) to calculate Type III F-statistics and P-values for my main, interacting terms and co-variate. In conjunction, I analyzed how movement rate between my four species was affected by temperature using a two-way ANOVA, with taxon, temperature, and their interaction as the fixed factors and again calculated Type III F-statistics and P-values.

I used mixed effect Cox proportional hazard regressions (using the ‘coxme’ function in the *coxme* package) to determine how prey survival (*C. lactis* and *F. candida*) differed under 16 °C and 24 °C while under risk of predation by *S. scimitus*, with temperature, prey and their interaction as the fixed effects using *C. lactis* at 16 °C as the baseline measurement. I did not include *O. nitens* in the choice or no choice Cox regressions as predator mites did not consume a single individual of *O. nitens* in either feeding trial at both temperatures. I ran separate Cox regressions for my choice and no choice feeding trials and used arena number as the random effect due to lack of independence between samples (i.e., prey survival may differ between individual arenas). For the Cox regressions, I reported the hazard ratio (and 95% confidence intervals), and corresponding P-values for each factor. Hazard ratios above 1 equates to prey survival probability being lower, relative to the baseline. Conversely, hazard ratios below 1 is equal to prey survival probability being higher, relative to the baseline. In addition, I compared survival curves by partitioning the data and running individual mixed effect Cox regressions for each pairing of treatments and corrected the p-values for individual tests using a Bonferroni correction. I plotted prey survival probability using Kaplan-Meier survival curves. Finally, I used Kruskal-Wallis Rank Sum test (using the ‘kruskal.test’ function in base R) to determine if temperature significantly affected the estimated energy intake of predators during the choice feeding trials.

2.3 Results

I found that *S. scimitus* produced more CO₂ at 24 °C than at 16 °C ($F_{1,6} = 11.69$, $P = 0.014$; Figure 2-1; Appendix A; Figure 1A) and therefore had higher metabolic demands under warming. I estimated the energy requirements for *S. scimitus* individuals during the feeding trials maintained at 16 °C to be 9.6 mJ 8 h⁻¹ individual⁻¹, which was

~30% lower than that of their counterparts maintained at 24 °C (12.2 mJ 8 h⁻¹ individual¹).

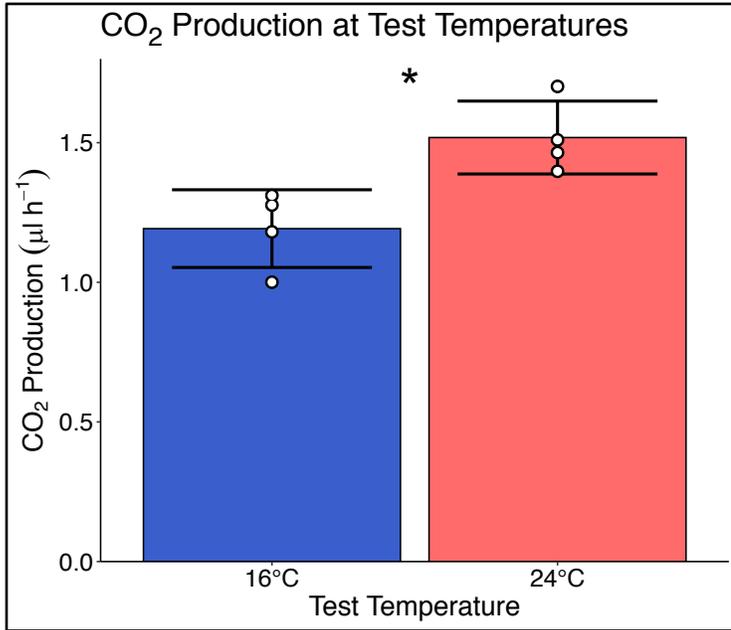


Figure 2-1 CO₂ production of *S. scimitus* maintained and tested at 16 °C and 24 °C (i.e., same conditions as the feeding trials).

*** indicates P < 0.05. Bars represent mean ± SD, while points are data values.**

I found that total protein content did not differ between 24 °C and 16 °C ($F_{1,15} = 1.28$, $P = 0.276$), but that *F. candida* had the highest protein content at both 16 °C and 24 °C ($F_{3,15} = 12.63$, $P < 0.001$). In addition, the interaction between taxon and temperature was also not significant ($F_{3,15} = 0.389$, $P = 0.763$; Figure 2-2A). Conversely, I found that total lipid content for all four taxa was lower at 24 °C than at 16 °C ($F_{1,14} = 24.14$, $P < 0.001$), but did not significantly differ among taxa ($F_{3,14} = 2.44$, $P = 0.107$), nor was the taxon \times temperature interaction significant ($F_{3,14} = 0.80$, $P = 0.512$; Figure 2-2B)

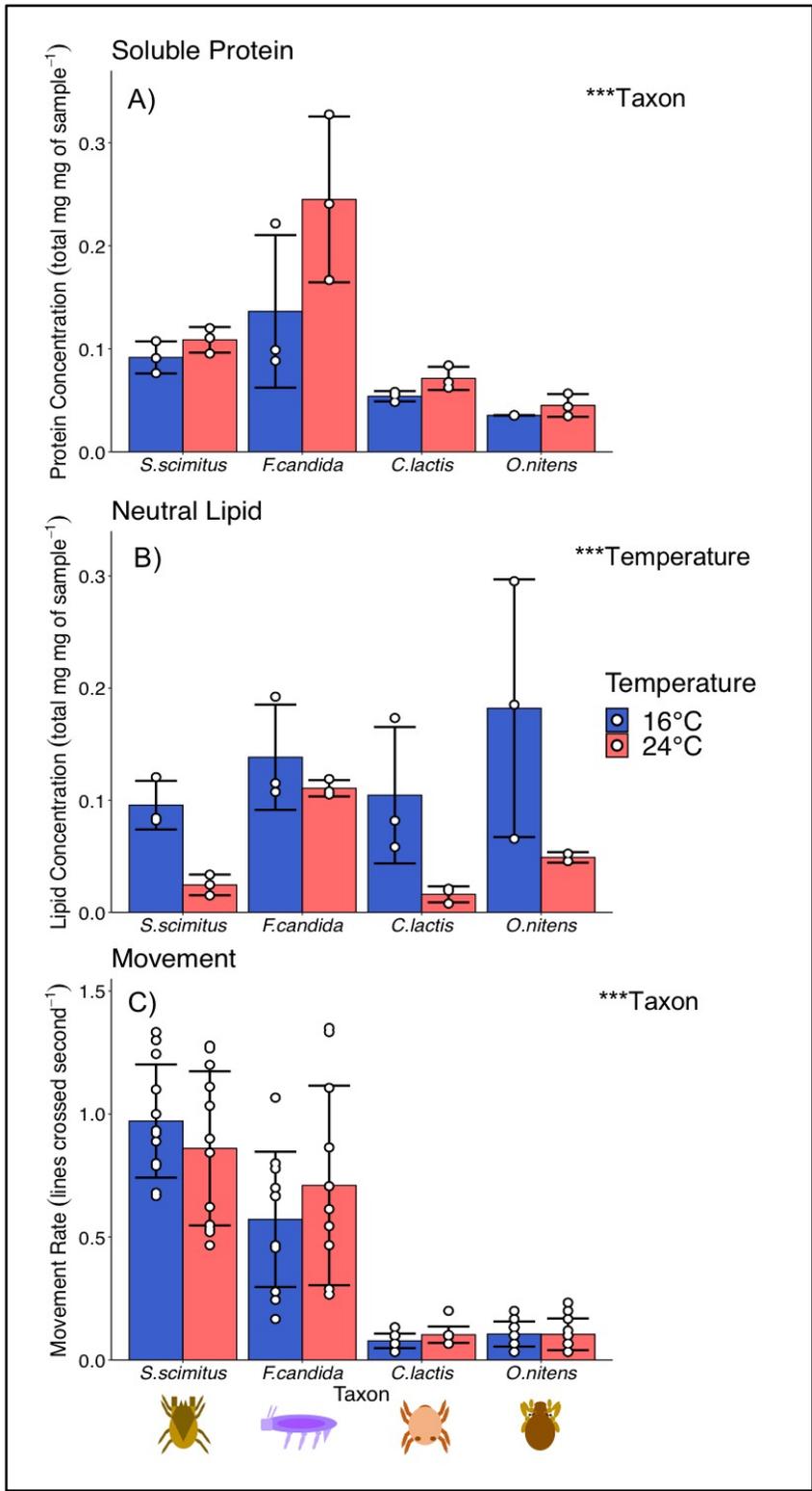


Figure 2-2 A) Soluble protein, B) neutral lipid, and C) movement of taxa (*S. scimitus*, *F. candida*, *C. lactis*, *O. nitens*) at 16 °C and 24 °C.

***** indicates $P < 0.001$. Bars represent mean \pm SD, while points are data values. I presented the mass-specific soluble protein and neutral lipid for ease of display, but statistical analyses were performed as an ANCOVA with sample mass as covariates.**

Using mean soluble protein and neutral lipid concentrations at each temperature, I estimated that *F. candida* had the highest energy content at both 16 °C and 24 °C, and that energy content (and subsequently energy density) decreased for all species, except *F. candida*, at 24 °C (Table 2-1). This decrease in energy content under warming for *S. scimitus*, *O. nitens*, and *C. lactis* was driven by lower lipid concentrations at 24 °C, but this was offset in *F. candida* as their protein concentrations rose considerably under warming. *Folsomia candida* body mass (28.7 µg) was considerably greater than the average body mass of *C. lactis* (3.76 µg) and *O. nitens* (17.4 µg), respectively, and a single *F. candida* consequently contained more energy than the other species; however, energy content was also temperature-dependent. The total energy content of *F. candida* at 16 °C was 11.8 times greater than *C. lactis* and 1.6 times greater than *O. nitens*. At 24 °C, energy content of *F. candida* was 35.1 times greater than *C. lactis* and 5.3 times greater than *O. nitens*.

1 **Table 2-1 Estimated body mass, and lipid and protein concentration of taxa (*S. scimitus*, *F. candida*, *C. lactis*, *O. nitens*) used to**
 2 **calculate energy content, and energy density at 16 °C and 24 °C.**
 3 **I calculated energy content by assuming an energy density of 17.8 J mg⁻¹ for protein, and 39.3 J mg⁻¹ for lipid (Schmidt-**
 4 **Nielsen, 1990).**

Taxa	Estimated Body Mass (µg)	Temperature (°C)	% Lipid	% Protein	Energy Content (mJ individual ⁻¹)	Energy density (mJ µg ⁻¹)
<i>S. scimitus</i>	38.3	16	9.6	9.2	207.2	5.4
		24	2.4	10.9	110.4	2.9
<i>F. candida</i>	28.7	16	13.8	13.6	225.1	7.8
		24	11.0	24.5	249.2	8.7
<i>C. lactis</i>	3.76	16	10.5	5.4	19.1	5.1
		24	1.6	7.1	7.1	1.9
<i>O. nitens</i>	17.4	16	18.2	3.5	135.3	7.8
		24	4.9	4.5	47.4	2.7

5

Movement rate differed significantly among taxa ($F_{3,86} = 82.33$, $P < 0.001$) with the predator *S. scimitus* fastest at both 16 °C and 24 °C, followed by *F. candida* (Figure 2-2C). I found that the average movement rate of *S. scimitus* was approximately nine times faster than that of the other mites at both temperatures. Movement rate did not change significantly with temperature, with all taxa exhibiting similar movement between 16 °C and 24 °C ($F_{1,86} = 0.078$, $P = 0.78$), while the interaction between temperature and taxon was also not significant ($F_{3,86} = 1.24$, $P = 0.299$).

Stratiolaelaps scimitus did not consume any *O. nitens* in either the choice or no choice feeding trials. Although I observed *S. scimitus* attacking *O. nitens* at both temperatures, it failed to successfully feed, likely because of their heavy sclerotization. The collembolan *F. candida* had a higher survival probability than *C. lactis* in both the choice (Prey_{*F. candida*}, HR = 0.23, 95% CI = 0.11 to 0.47, $P < 0.001$) and no choice (Prey_{*F. candida*}, HR = 0.13, 95% CI = 0.07 to 0.25, $P < 0.001$) trials (Figure 2-3). Moreover, in both choice (Temperature_{24°C}, HR = 2.89, 95% CI = 1.59 to 5.27, $P < 0.001$) and no choice (Temperature_{24°C}, HR = 3.34, 95% CI = 2.12 to 5.27, $P < 0.001$) trials, a higher temperature decreased the survival of *C. lactis* prey species, with no effect on the survival of *F. candida* leading to a significant interaction between prey and temperature (choice: Prey_{*F. candida*}×Temperature_{24°C}, HR = 0.14, 95% CI = 0.042 to 0.435, $P < 0.001$; no choice: Prey_{*F. candida*}×Temperature_{24°C}, HR = 0.26, 95% CI = 0.10 to 0.66, $P = 0.005$). As *C. lactis* are slow, small-bodied, and lack defenses, individuals had no mechanism to defend against attacks from *S. scimitus*, making them an easy target for predators. Conversely, because of their larger size, faster movement and defenses (i.e., an appendage used for jumping) *F. candida* was fed upon less by *S. scimitus* and could repel against attacks from predators. I also observed that predators frequently abandoned captured *F. candida* at 24 °C, leading to partial prey consumption of their large-bodied prey, but this was not observed with the small-bodied prey *C. lactis*.

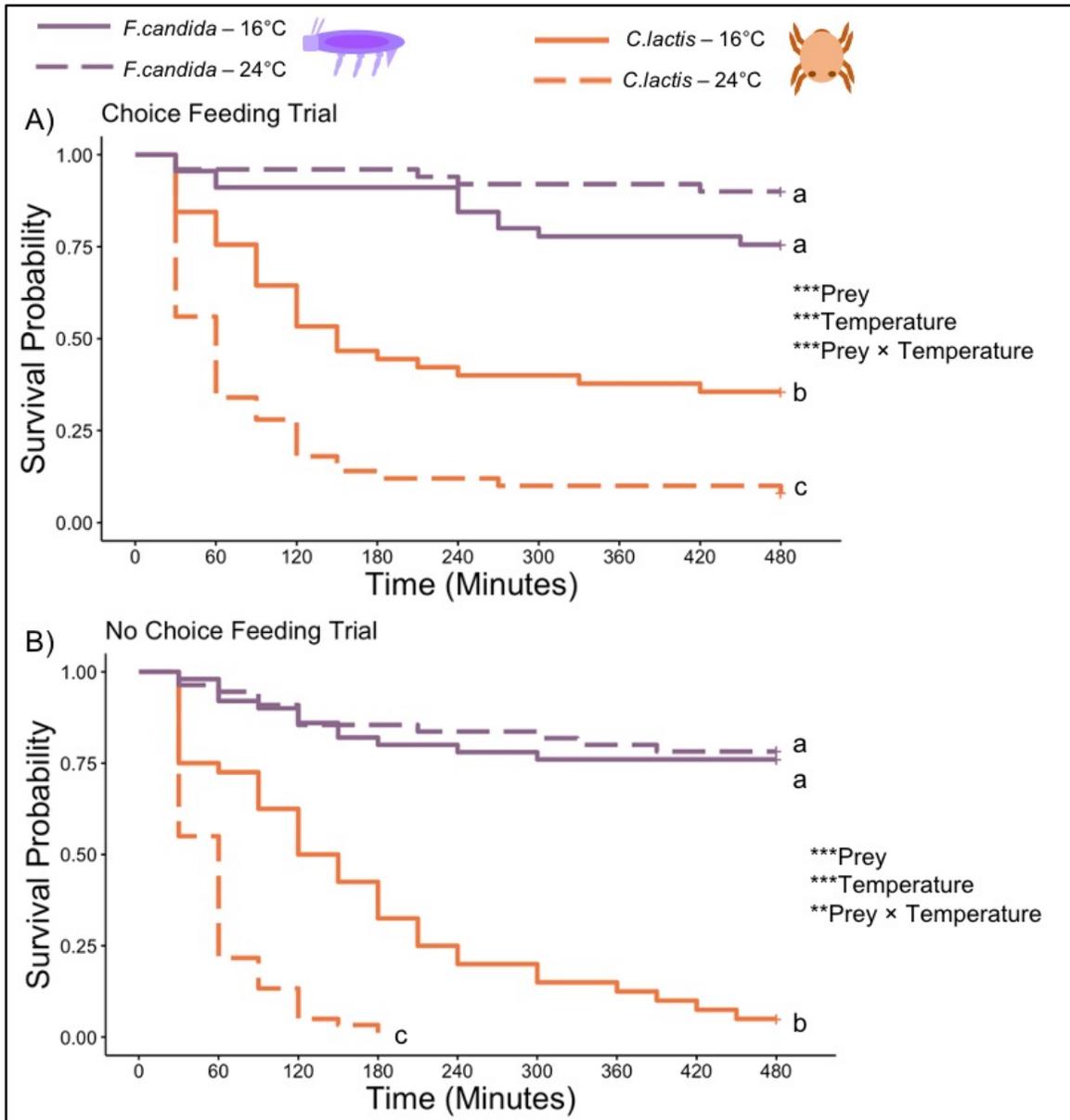


Figure 2-3 A) Choice and B) no choice feeding trials showing the survival probability of *C. lactis* and *F. candida* being fed on by *S. scimitus* at 16 °C and 24 °C. *S. scimitus* did not feed on any *O. nitens* individuals in either feeding trials or temperatures and were therefore excluded from my analyses. I used *C. lactis* from 16 °C cultures as the baseline treatment for both the choice and no choice feeding trials mixed effect Cox regressions. ** indicates P-value < 0.01, * indicates P-value < 0.001. Letters indicate significant differences (P < 0.05) between treatments after a Bonferroni correction.**

Finally, I estimated that the energy intake for *S. scimitus* individuals was significantly higher at 16 °C (Kruskal Wallis test: $H = 6.91$, $df = 1$, $P = 0.009$; 80.89 ± 24.30 mJ 8 h⁻¹ individual⁻¹; mean \pm SD; Figure 2-4), compared to the energy intake at 24 °C (30.55 ± 30.31 mJ 8 h⁻¹ individual⁻¹). This was mainly due to the slight decrease in feeding rate of *S. scimitus* on *F. candida* at 24 °C, along with the lower energy density of *C. lactis* individuals at 24 °C. This resulted in estimated energy intake by *S. scimitus* being 8.3 times greater than their energy requirements during the feeding trials at 16 °C, but only 2.5 times greater at 24 °C.

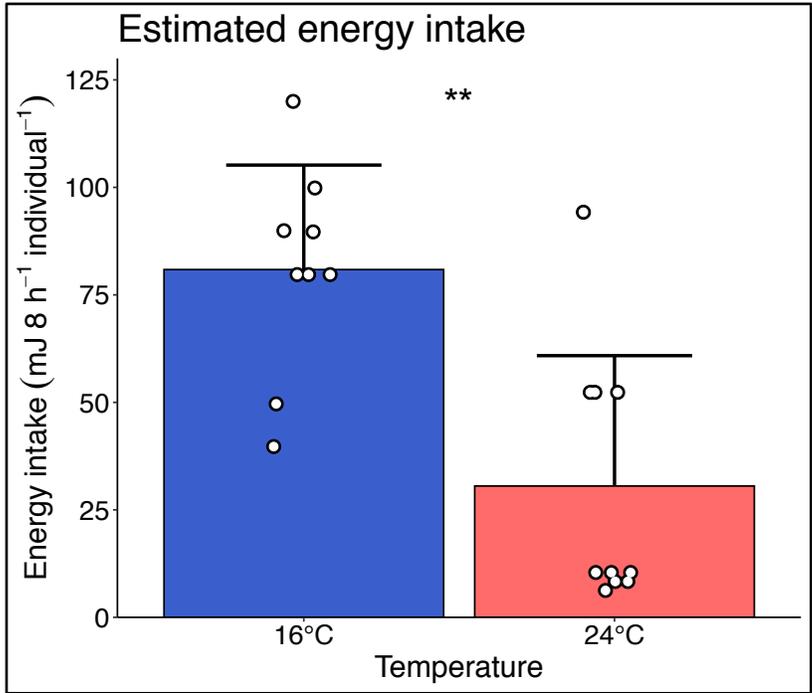


Figure 2-4 Estimated energy intake of *S. scimitus* during the choice feeding trials at 16 °C and 24 °C.

**** indicates $P < 0.001$. Bars represent mean \pm SD, while points are data values.**

2.4 Discussion

Climate warming could affect predator-prey dynamics by increasing the metabolic demands of predators, which could drive novel feeding rates and behaviours as predators navigate trade-offs in prey selection, including changes in energy content, handling time, and body size (among other functional constraints). I found that increasing the temperature from 16 °C to 24 °C increased the CO₂ production of my predator, *S. scimitus*, by ~30%, but predators energy intake was greater at 16 °C than 24 °C. The predator *S. scimitus* lowered the survival rate of the small-bodied prey, *C. lactis*, at 24 °C in both the choice and no choice trials. However, the survival rate of the large-bodied prey, *F. candida*, did not significantly change with temperature. As well, the energy density of *C. lactis* was lower at 24 °C (compared to 16 °C), but marginally increased for *F. candida* at 24 °C. I also observed that capturing and handling of *C. lactis* by predators was far less strenuous than with *F. candida* at both temperatures due to differences in their body size and defenses (for more details on my observations, see section 2.4.1 below). Together, these results and observations strongly support my second hypothesis that under climate warming, predators may minimize energy lost during feeding, which in this case, consists of favouring the small, easy to capture *C. lactis*. Predators should select prey based on cost-benefit trade-offs of energetic gains and losses. Therefore, I interpret my results to be that differences in energy content and ‘capturability’ (i.e., body size, movement rates) of *C. lactis* and *F. candida* lead to the novel feeding rates and behaviours observed under warming. *Carpoglyphus lactis* is energy-poor compared to *F. candida*, but is smaller, slower, and has no defenses making *C. lactis* easier to capture and consume under increased metabolic demands. Conversely, because of their larger size, faster movement and defenses (i.e., an appendage used for jumping) *F. candida* could repel against attacks from *S. scimitus*, making *F. candida* harder to capture.

In both my choice and no choice feeding trials, I found that predators increased their feeding on small-bodied prey, which has been observed with other ectothermic predators, like dragonfly larvae and fish (Dobashi et al., 2018; Frances and McCauley, 2018). This can be attributed to smaller animals typically being slower than larger

animals (making them easier to catch; Hirt et al., 2017) and require less time to capture and handle (Brose et al., 2008; Rall et al., 2012). My results are also similar to Jensen et al. (2019) who also found that predator mite feeding rate on ‘easy’ prey (i.e., a slower moving collembolan) increased more under warming than when feeding on faster collembolan prey, which were likely harder to catch. Ectothermic predators can increase their feeding rates under warming to compensate for higher metabolic demands. But energetic efficiency (i.e., the *per capita* feeding or ingestion rate divided by metabolic rate) can decrease at higher temperatures as metabolic rate increases faster than feeding rates (Rall et al., 2010; Vucic-Pestic et al., 2011). As a result, even modest increases in metabolic demands for predators may lead to novel feeding rate and behaviours to limit energetic losses. I theorize that predators selected the small-bodied, easy to capture prey under warming because predators prioritized lower handling costs to combat higher metabolic demands instead of maximizing energetic gains associated with larger prey. Even though predators could have captured and fed more on large-bodied prey at 24 °C, it appears predators preferred feeding on small-bodied prey under warming (see section 2.4.1 below for more details on predator feeding behaviour). As a result, energy intake decreased as predators traded-off higher energy gains for lower energy losses.

Along with being the most energy-rich prey (due to its large body size), *F. candida* was also the most energy-dense prey. Predator mites feeding on a single *F. candida* at 16 °C and 24 °C was equivalent to feeding on four (at 16 °C) or 20 (at 24 °C) *C. lactis* individuals. This dramatic change in feeding equivalency of prey between the two temperatures primarily stems from the reduced energy density (driven by the reduced lipid concentration) of *C. lactis* at 24 °C. Reductions in the energy density of *C. lactis* at 24 °C contributed to the lower energy intake during the choice feeding trials, as predators would need to consume more *F. candida* to compensate for this decrease. I found that predator mites often exhausted *C. lactis* prey at 24 °C but did not increase their feeding *F. candida*. Despite apparent deficiencies in energy intake, the reluctance of predators to feed on *F. candida* under warming may stem from the aforementioned differences in capturability and handling of each prey item and resulted in lower energy intake for predators.

I calculated a lower energy intake for *S. scimitus* at 24 °C, compared to 16 °C during the choice feeding trials, but this estimated energy intake still exceeded the calculated energy requirements for the predators. Nevertheless, there may be long-term consequences for decreased energy intake for predators under climate change. Already, predators have lower starvation tolerance at higher temperatures as individuals lay relatively fewer eggs when food deprived under warming (Jensen et al., 2018, 2017). Predators could compensate for this by accumulating energy stores (Jensen et al., 2010). However, in my study, *S. scimitus* maintained at 24 °C had less body lipid content than at 16 °C and did not increase consumption on the more energy-rich prey, *F. candida*, suggesting that *S. scimitus* are not accumulating energy stores and may therefore have less of a safety margin for missed feeding opportunities at higher temperatures. Decreased starvation tolerance and lower reproductive output for predators may lead to decreased population size, exposing them to greater extinction risk (Cardillo, 2003) alongside increased susceptibility to other disturbances.

Climate change strengthens top-down control by predators through increased feeding rates (Barton et al., 2009; Ramachandran et al., 2021; Tanentzap et al., 2020; Walker et al., 2020), and an increased consumption of small-bodied prey (as I show here) can further alter food web dynamics as a predator-prey mass ratio is positively correlated with interaction strength but negatively correlated with trophic transfer efficiency (Barnes et al., 2010; Emmerson and Raffaelli, 2004). Increased consumption of smaller, energy-poor prey may also alter prey community composition, increasing the prevalence of large-bodied prey (Yvon-Durocher et al., 2015). However, I found that the well-defended medium-sized prey in my study, *O. nitens*, was not consumed at either test temperature. This suggests that increased energy demands for *S. scimitus* did not change the prey species that predators can feed on. Furthermore, this implies that well defended prey species (via chemical and physical defenses, or both) will be largely unaffected by higher predator feeding rates. As prey defenses can control the strength of top-down trophic cascades (Van der Stap et al., 2007), the presence (or absence) of defended prey may partly dictate how predators restructured food webs under climate change.

2.4.1 Observations during the feeding trials

During feeding trials, observations of *S. scimitus* revealed particular behaviours, some of which appear to be undocumented. While mesostigmatic mite feeding styles and behaviour appears to be similar across species (Ali and Brennan, 2000; Bowman, 1987; Eveleigh and Chant, 1981; Flechtmann and McMurtry, 1992; Muraoka and Ishibashi, 1976), I observed some distinctions in feeding behaviour by predators when attacking *F. candida* versus *C. lactis*, stemming from the differences in their body size. For *F. candida*, my predators used tarsi of leg I to detect prey and if attacking, would ‘lunge’ at their prey using legs I and II to entrap individuals. Afterwards, mesostigmatic individuals would pierce and tear apart prey using their chelicerae to feed. As fluid-feeders, predators become larger as fluids flow from prey to predator as they imbibe digested prey (Bowman, 2014). When predators consumed entire *F. candida* individuals, feeding took several hours and often required resting periods; *S. scimitus* individuals would stop feeding, drop prey, but return later to continue feeding (Bowman, 1987). For *C. lactis*, *S. scimitus* individuals still used tarsi I to detect prey but if attacking, would only use their chelicerae to pick up prey and did not require the use of either legs I or II. As well, feeding on a *C. lactis* individual took considerably less time, and therefore energy, than feeding on *F. candida*. When predators had finished feeding on *F. candida* and *C. lactis* individuals, prey bodies were shrivelled and abandoned.

Interestingly, I observed that predators would attack and capture both *F. candida* and *C. lactis* individuals but feeding would not commence until predators had moved prey individuals to secluded parts of the arena. This behaviour is not unlike chickadees (as one example) who carry food to protective areas to feed, away from potential predators (Lima, 1985). This behaviour further exacerbates the energy demands of predators feeding on *F. candida* versus *C. lactis*, particularly on larger *F. candida*. I observed that for *S. scimitus* individuals, carrying *F. candida* appeared to be strenuous, and more effort was required to move *F. candida* individuals to secluded areas to feed. Conversely, I observed that when predators were carrying *C. lactis* movement was unhindered, as individuals did not appear slower than if not handling the prey. To my knowledge, this is the first documented observation of a mesostigmatic mite species

moving prey to secluded areas before feeding commenced, representing a new behavioural trait for the group.

As mentioned, it appears predators preferred feeding on small-bodied prey under warming because predators increased feeding on *C. lactis* but did not increase their feeding on *F. candida* under warming. This was not because predators could not capture and handle the larger prey at the higher temperatures (i.e., prey had higher escape efficiency), although follow up experiments showed that *S. scimitus* had lower capturing ability for large *F. candida* at 24 °C compared to 16 °C. However, I often observed that predators would capture *F. candida* and then drop the individual before feeding had even commenced despite the abandoned *F. candida* prey appearing injured and undefended. Together, this strengthens my argument that predator feeding rate and behaviour under warming was driven by trade-offs in the handling costs associated with *F. candida* versus *C. lactis* at 24 °C, as predators could capture *F. candida* at the higher temperature but did not feed more on those individuals under warming, possibly due to the energy require to move larger *F. candida* to a secluded feeding spot.

Stratiolaelaps scimitus did not feed on a single *O. nitens* during the feeding trials, at either temperature. Similar to *F. candida* and *C. lactis*, predators would use tarsi I to detect *O. nitens* and then attack, but predators were not successful in capturing individuals due to the sclerotization of *O. nitens* body. I found that predators would attack multiple times over the course of the trials, but again were never successful. Adult oribatid mites live in ‘enemy-free space’ as individuals contain an array of defensive mechanisms (e.g., sclerotization, chemical cues, protective setae) (Brückner et al., 2017; Peschel et al., 2006) that protect and deter attacks from soil predators. As *S. scimitus* could not overcome *O. nitens* defenses, it provides further evidence that adult oribatid mites are an uncommon prey group for mesostigmatic mites in soil systems.

2.4.2 Caveats and limitations

There are always caveats and limitations when considered the results of a predator-prey experiment within a broader ecological context. Because of the parabolic relationship between predator-prey mass ratio and feeding rate (Brose et al., 2008), changes to prey body size preferences for predators is possibly context-dependent, based

on the available prey and predator body size. If offered other species, *S. scimitus* may have abandoned both small- and large-bodied prey in favour of a intermediate-sized prey (i.e., a prey similar in size to *O. nitens* that does not have defensive mechanisms) to maximize their feeding rates, changing my underlying conclusions and interpretations. Potentially, using different-sized individuals of the same prey species (e.g., *F. candida*) may better detect the effect of prey body size on predator feeding behaviour.

Using simplified invertebrate predator-prey systems allowed me to test hypotheses and explore how ectothermic predator feeding changes at higher temperatures. However, direct measurements of energy intake, along with energy spent capturing, handling, and digesting (i.e., specific dynamic action) of prey during the feeding trials were not possible. Because of this, I am unable to quantify the net energy intake of predators (i.e., subtracting total energy ingested from total energy losses) which would strengthen my conclusions. Similar studies have also used the average weight and energy density of their prey to calculate energy gains for predators (Rall et al., 2010; Sentis et al., 2012; Sohlström et al., 2021; Vucic-Pestic et al., 2011), but I expanded that work to include an empirical measurement of change in body mass in my energy intake formula. This is still an indirect measurement of energy intake but it provides additional evidence of the consequences of changing feeding behaviour for ectothermic predators under warming. While I hypothesized long-term consequences of changing feeding behaviour for predators, further examination at the population and community level under longer-term or natural conditions is warranted.

2.4.3 Conclusions

Climate warming is anticipated to have both direct and indirect effects on species at physiological, behavioural, and population levels with cascading effects on community composition, diversity, and ecosystem processes. I showed that warmer temperatures may increase top-down control on some ectothermic predator-prey interactions, but weaken others, and that prey body size, defense tactics, and handling time are important factors in predator-prey dynamics under climate warming. I found that predators increased feeding on small-bodied, energy-poor prey in favour of large-bodied, energy-rich prey under warming, but that energy intake was lower at the higher temperature.

Thus, predators may prioritize minimizing handling costs over maximizing energy gains when feeding under greater metabolic demands with climate warming.

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Chapter 3

3 Species interactions are less sensitive than population size to temperature change and variability in a predator-prey ectotherm model system

3.1 Introduction

Climate change is increasing the mean and variability of temperatures as extreme warming events, like heat waves, are becoming more frequent, prolonged, and intense (IPCC, 2021; Perkins-Kirkpatrick and Gibson, 2017). Rising temperatures will disrupt ecological communities as nearly all organisms (i.e., ectotherms) respond to temperature change. Ectotherms rely on external heat sources to regulate their body temperature (Clarke, 2017). As a result, environmental temperatures are tightly coupled to their individual metabolic and physiological rates that govern movement, growth and feeding (hereafter grouped as ‘performance’) (Deere and Chown, 2006; Kingsolver et al., 2015; Lemoine and Burkepile, 2012). This temperature-performance relationship for ectotherms follows a predictable pattern and is often described using a thermal performance curve (TPC; see Figure 1-1 for example of TPC). Ectotherm performance starts at a critical minimum temperature (CT_{min}) and increases curvilinearly until the thermal optimum (T_{opt}), before declining rapidly towards a critical maximum temperature (CT_{max}) (Angilletta Jr, 2009; Sinclair et al., 2016). The general shape of TPCs can be species-, and even function (performance)-specific (Rezende and Bozinovic, 2019; Stevenson et al., 1985), as such, whether warming (or cooling) is beneficial for an ectotherm’s overall performance is highly contextual.

Ectotherm populations, communities and their underlying interactions, like predation, are temperature-sensitive (Dell et al., 2014, 2011; Gilbert et al., 2014), meaning climate change will both directly (changes to metabolic and physiological rates) and indirectly (changes to species interactions) affect ectotherms. Ectothermic predators and their prey may exhibit different responses to temperature change as conditions that are detrimental to prey may benefit predators, and vice versa, creating a thermal

mismatch. For example, a predator's CT_{max} can exceed their prey (de Mira-Mendes et al., 2019; Franken et al., 2018; Pintanel et al., 2021), meaning predators can function (and subsist) at warmer temperatures. Predator-prey thermal mismatches may lead to outcomes not predicted at cooler temperatures (Grigaltchik et al., 2012; Öhlund et al., 2014) further complicating how increasing temperature mean and variability will disrupt ectotherm populations and communities.

Our understanding of how climate change affects ectotherms is limited as most studies have focused on the effect of rising average temperatures, and not temperature variability. This includes individual-level functions like feeding (e.g., Cuthbert et al., 2021; Daugaard et al., 2019; Twardochleb et al., 2020; Zhang et al., 2020), population-level dynamics related to predator-prey interactions (e.g., Thakur et al., 2018, 2017), and on communities and whole food webs (e.g., Dossena et al., 2012; Kratina et al., 2012; Seifert et al., 2015; Shurin et al., 2012; Yvon-Durocher et al., 2015, 2011). Temperature variability under relatively cool or warm conditions may yield different outcomes. For example, with the mosquito species *Anopheles stephensi*, Paaijmans et al. (2013) found variability around a cool mean temperature (18 °C) was beneficial as developmental rate and survival probability increased, but detrimental around a warm temperature mean (32 °C) as both subsequently decreased. This is a result of the non-linear relationship between temperature and ectotherm performance, and is why incorporating both increasing mean temperature and variability is needed to fully comprehend how ectotherms may respond to climate change (Bernhardt et al., 2019; Dee et al., 2020; Kingsolver et al., 2015; Marshall et al., 2021; Morash et al., 2018). For instance, Vasseur et al. (2014) using TPCs found that both increasing mean and variance of temperature more accurately portrayed how climate change will affect ectotherm performance, than increasing mean alone. Together, temperature variability will significantly impact ectotherm performance, but also ectotherm populations and communities.

In this study, I used microarthropods to test how changing mean and variability of temperature affects ectothermic predator-prey interactions at the population-level using mesocosms. Predators and prey were acclimated to a neutral temperature (20 °C) before examining population-level predator-prey interactions across a cool (12 °C to 20 °C) and warm (20 °C to 26 °C) temperature range. To assess how temperature variability affects

predator-prey interactions, I measured population (total predator and prey abundance), trait-based (average predator and prey body length, and prey body length distribution), and predator-prey indices (predator-prey mass ratio (PPMR) and interaction strength). I have three sets of hypothesis and predictions, one each for the prey and predators, and the other for the predator-prey interactions. In my experiment, I hypothesize that if increased exposure to 20 °C from 12 °C improves performance for both predators and prey, then predator and prey (when predators are absent) abundances will increase, and predator-prey interactions will strengthen. But conversely, I hypothesize that if increased exposure to 26 °C from 20 °C is detrimental to both predators and prey, then predator and prey abundances will decrease, while predator-prey interactions will also weaken.

3.2 Methods and Materials

3.2.1 Predator and prey species

For my study, I used the mite species *Stratiolaelaps scimitus* (Arachnida: Mesostigmata: Laelapidae) as my predator and the collembolan species *Folsomia candida* (Hexapoda: Collembola: Isotomidae) as my prey. Predatory *S. scimitus* was purchased from Koppert Canada Limited (Toronto, ON, Canada) and maintained at 20 °C in complete darkness until the start of the experiment. *Stratiolaelaps scimitus* cultures were shipped in a vermiculite/peat mixture with the soft-bodied mite *Tyrophagus putrescentiae* as its prey. After one week, *T. putrescentiae* was exhausted from predator cultures, thereafter, I supplemented predator diet with adult and juvenile *F. candida*. I used stock cultures of *F. candida* that have been maintained at Western University (London, ON, Canada) since 2011. *Folsomia candida* populations have been maintained on 9:1 plaster-of-Paris and activated charcoal substrate at room temperature (~20 – 22 °C) and natural diurnal light cycles, with a diet consisting of dried yeast pellets (Active Dry Yeast, Fleischmann's Lasalle, QC, Canada).

Both *S. scimitus* and *F. candida* reproduce via parthenogenesis (asexual reproduction). *Folsomia candida* populations consist entirely of female individuals (Fountain and Hopkin, 2005), while *S. scimitus* reproduction strategy is arrhenotokous parthenogenesis, where males are reproduced asexually and females sexually (Norton et al., 1993). With respect to *F. candida*, at 20°C, their eggs hatch 7-10 days after egg

deposition while individuals reach sexual maturity after another 21-24 days, meaning the generation time is roughly 28-34 days (Fountain and Hopkin, 2005). In my own populations, I found that the generation time was ~28 days when *F. candida* are maintained at room temperature. But similar to other ectotherms (Gillooly et al., 2002; Savage et al., 2004), warming affects the life-history of both species. The average lifespan of a *F. candida* individual at 15 °C (241 days) is 3.3× longer than at 26 °C (72 days) (Snider and Butcher, 1973), while egg production is also higher at cooler temperatures, as individuals produced, on average, 1344 eggs at 15 °C, but only 130 eggs at 26 °C during their lifetime. For *S. scimitus*, average egg-to-adult (time spent as a juvenile) period for females was 3.5× longer at 25 °C (13 days) compared to 15 °C (46 days) (Ydergaard et al., 1997), but, the average lifespan for an individual mite was 2.5× longer at 15 °C (89 days) versus a mite at 25 °C (39 days).

The optimal temperature (T_{opt}) for *F. candida* is likely lower than *S. scimitus*. Although both species exhibit faster individual growth rates under higher temperatures, historically, optimal temperature for *F. candida* was recorded at ~20 °C (Snider and Butcher, 1973). In conjunction, after several weeks of exposure to five temperatures (6 °C, 11 °C, 16 °C, 21 °C, and 26 °C), *F. candida* juvenile population density was highest at 21 °C, while adult population density peaked at 16 °C as both adult and juvenile density decreased at 26 °C (Mallard et al., 2020). Conversely, *S. scimitus* has maximum egg production (number of eggs laid day⁻¹) at ~25 °C (Ydergaard et al., 1997), while *S. scimitus* populations were of similar size when maintained at 21 °C and 28 °C after forty days (Wright and Chambers, 1994). Within the context of my experiment, these studies suggest that *F. candida* has a lower T_{opt} than *S. scimitus* which will likely impact predator-prey interactions, particularly in the warm temperature range.

3.2.2 Experimental design

I had two temperatures ranges in my study, a cool (12 °C to 20 °C) and a warm (20 °C to 26 °C) temperature range with five different exposure times to each temperature in 8-day cycles (Appendix B; Figure 2B). The cool temperature range included:

A) 8:0 split — 8 days at 12 °C : 0 days at 20 °C (i.e., constant 12 °C),

B) 6:2 split — 6-days at 12 °C : 2-days at 20 °C

C) 2:2 split — 2-days at 12 °C : 2-days at 20 °C (i.e., predators and prey spent 2-days at 12 °C, 2-days at 20 °C, then repeated this to complete one 8-day cycle)

D) 2:6 split — 2-days at 12 °C : 6-days at 20 °C, and

E) 8:0 split — constant 20 °C

The warm temperature range included a similar design:

A) 8:0 split — constant 20 °C

B) 6:2 split — 6-days at 20 °C : 2-days at 26 °C

C) 2:2 split — 2-days at 20 °C : 2-days at 26 °C

D) 2:6 split — 2-days at 20 °C : 6-days at 26 °C, and

E) 8:0 split — constant 26 °C

Because of the experimental design, the average temperature within each treatment was different. In the cool temperature range, average temperature for 8:0 treatment – 12 °C, for 6:2 – 14 °C, for 2:2 – 16 °C, for 2:6 – 18 °C, and for 0:8 – 20 °C. In the warm temperature range, average temperature for 8:0 treatment – 20 °C, for 6:2 – 21.5 °C, for 2:2 – 23 °C, for 2:6 – 24.5 °C, and for 0:8 – 26 °C.

To tease apart the effect of predation on prey populations, I also had a predator addition treatment, where predators were either present or absent from mesocosms, which led to a total of 80 experimental replicates (5 levels of exposure time × 2 temperature ranges × 2 levels of predator addition × 4 replicates = 80). I conducted my experiment across two sampling periods, separated by experimental temperatures (12 °C to 20 °C between February 8, 2021 – March 20, 2021, and 20 °C to 26 °C between October 22, 2021 – December 1, 2021). One caveat of running the experiment across two time points is that predator and prey population cycles may vary between the two temperature ranges, even though there are overlapping treatments (i.e., 20 °C constant) and the same criteria was used to select predator and prey individuals (for more details on selection criteria, see below). Because of this, innate differences in predator and/or prey population size between the two temperature ranges needs to be considered. I removed one sample from the warm temperature range (20 °C constant, predators absent) after the experiment had concluded due to mishandling and spilling the sample, leaving 79 samples intact. Using values attained in Chapter 2, I estimated the metabolic ($J\ 40\ \text{days}^{-1}$

individual⁻¹) and consumption rate (number of *F. candida* eaten 40 days⁻¹) of *S. scimitus* during the experiment for each temperature treatment (Appendix B).

My mesocosms consisted of a hermetically sealed 500 ml glass mason jar, which contained a substrate of plaster of Paris and active charcoal (9:1 ratio) (Appendix B; Image 1B). Prior to the experiment, I moistened the substrate until water pooled on top. I then added in 7 g of vermiculite to each mesocosm, and subsequently 7 g of water to the vermiculite itself. I provided 15 mg of dried yeast pellets to each mesocosm at the start of the experiment to supplement collembolan diets. I then placed 22 individuals of *F. candida* (of which their body length was approximately 1000 µm in size) within each mesocosm. In half the mesocosms I added 5 adult *S. scimitus* (1 predator : 4.4 prey ratio). This starting ratio of predators to prey is similarly to that of Thakur et al. (2018, 2017) (1 predator : 3.3 prey) who used a similar experiment design. This starting ratio is also roughly equivalent to the ratio of arthropod-feeding mesostigmatic mites to collembolans I found in my 12 °C mesocosms used in Chapter 4. I systematically added predator and prey individuals to each mesocosm in the order of temperature treatment (A – E) listed above, alternating between predator and predator-free mesocosms.

My experimental mesocosms were maintained in three separate apparatuses. I used a Isotemp Laboratory Refrigerator from Fisher Scientific (Ottawa, ON, Canada) to maintain the mesocosms at 12°C (± 1°C), a GCHA-10 Environmental Growth Chamber (Chagrin Falls, OH, USA) for mesocosms at 20°C (± 0.5°C), and a B.O.D Low Temperature Incubator (Plainfield, NJ, U.S.A) for mesocosms at 26°C (± 0.5°C) to provide the best and most reliable temperature stability within a given temperature. For mesocosms that were exposed to more than one temperature I transferred them to the respective apparatus every two or six days. I also maintained the gravimetric moisture content by adding in water lost through evaporation every 8-days. Because I had an airtight seal, moisture loss from my mesocosms from evaporation was minimal. Typically, I added 0.1-0.5 grams of water to each mesocosm.

3.2.3 Sample processing

My experiment lasted for forty days (equaling five complete 8-day cycles). Whereafter I extracted predator and prey individuals for 3-days using Tullgren funnels

with 25-watt light bulbs, into 75% EtOH. I counted and measured the body length (in μm) of every *S. scimitus* and *F. candida* individual extracted using a Nikon SMZ 745T Dissecting scope with a DF-Fi2 camera attachment and NIS-Elements AR 4.20.01 software (Nikon Canada, Mississauga, ON, Canada). With these measurements, I calculated the average predator and prey body length within each mesocosm, as well as prey body length distribution for each temperature treatment.

Subsequently, I converted the body length of each predator and prey individual into body mass using two, taxa-specific formulas. For *S. scimitus*, I used the length-body weight formula for mesostigmatic mites reported in Mercer et al. (2001):

$$\log_{10}(Y) = 2.064 + (2.857 * \log_{10}(L)),$$

$$W = 10^Y$$

where Y is body mass in μg in logarithmic form, L is the length of the idiosoma (body length, excluding mouthparts) in mm, and W is anti-log weight in μg .

For *F. candida*, I used the length-body weight conversion formula as described by Edwards (1967):

$$W = (3.06 * L)^3$$

where W is body mass in μg , and L is the length of *F. candida* in mm. With this information I measured the predator-prey mass ratio within my mesocosms.

3.2.4 Predator-prey mass ratio

I calculated the predator-prey mass ratio (PPMR) within my predator addition mesocosms, across all temperature treatments to gauge how temperature shapes the relative body size between predators and their prey after 40 days together. With some exceptions, predators overwhelmingly consume prey smaller than themselves (Brose et al., 2019, 2006). PPMR captures the difference between predator and prey body size and is the magnitude that a predator is larger than its prey (Nakazawa et al., 2011). There are several definitions for PPMR that differ in resolution (see Nakazawa et al., 2011). I used the species-averaged PPMR calculated as:

$$\text{Species – averaged PPMR} = \frac{\text{Mean mass of predators within a mesocosm}}{\text{Mean mass of prey within a mesocosm}}$$

Species-averaged PPMR requires only average predator and prey body sizes and does not rely on individual-level feeding information and is considered the lowest resolution PPMR metric. However, species-averaged (or more broadly group-averaged) PPMR can detect differences in predator-prey body size ratios at higher ecological levels, like communities or whole food webs (Brose et al., 2006; Reczuga et al., 2018; Woodson et al., 2018) making it applicable for my study.

I calculated the \log_{10} ratio of average body mass (in μg) of predators : prey to gauge PPMR for each mesocosm where predators were present. In my study PPMR indicates the average mass of predators relative to their prey remaining in the mesocosms. Because of this, I cannot not fully disentangle the interaction between faster growing and developmental rates for ectotherms (Atkinson, 1994; Gillooly et al., 2002), with changing predator feeding behaviour (Frances and McCauley, 2018) on predator and prey body size. But combining PPMR with measurements of average predator and prey body length, I can infer mechanisms to explain potential changes to PPMR with temperature.

3.2.5 Interaction strength – Dynamic Index

I measured the predator-prey interaction strength to determine if predator-prey interactions became stronger (or weaker) under rising temperature mean and variability. Interaction strength is the effect of one species abundance on the abundance of another (Berlow et al., 1999; Wootton and Emmerson, 2005), as per capita interaction strength scales with the population size of each (Novak and Wootton, 2010). Interaction strength between and within individuals, populations, and entire food webs can be derived using numerous metrics (Berlow et al., 2004), but is often measured using the Dynamic Index (i.e., per capita interaction strength ; Wootton, 1997) that compares the abundances of prey with and without predators (McCluney and Sabo, 2009; O’Gorman et al., 2010, 2008; Storero et al., 2020). To measure predator-prey interaction strength, I used the Dynamic Index:

$$DI_{Tt} = \frac{\ln\left(\frac{P_{Tt}^+}{P_{Tt}^-}\right)}{D_{Tt}}$$

Where DI_{T_t} is the Dynamic Index for each temperature treatment T_t (A-E, listed in section 3.2.2), $P_{T_t}^+$ is the abundance of prey in the presence of predators in a mesocosm at temperature treatment T_t , $P_{T_t}^-$ is average abundance of prey when predators were absent at temperature treatment T_t , and D_{T_t} is average abundance of predators at temperature treatment T_t . Negative values equate to a decrease in prey population size when predators are present. The opposite is true for positive values – prey abundances increases when predators are present. Greater negative or positive values indicate greater interaction strength.

There are a several considerations when calculating interaction strength (Wootton and Emmerson, 2005). Over longer timescales, indirect effects (e.g., interactions between competitors) or density dependent feedbacks (e.g., habitat and population size) can develop and affect interaction strength. Due to the length of my experiment and the reproduction rate of my prey, more than one generation will co-exist within my mesocosms. On the outset of the experiment, initial consumption by predators will lower prey density, but also remove future individuals from populations due to lower total reproductive output. Meaning, predator-prey interaction strength in my study encapsulates both the direct (predators initial and continued feeding throughout the experiment) and indirect (lower total reproductive output due to fewer individuals) effect that predators have on their prey.

3.2.6 Statistical analysis

I performed all statistical analyses using the R statistical program (R Version 3.5.1; R Core Team 2018). For all statistical tests, I evaluated the underlying assumptions of each model. I analyzed my cool (12 °C to 20 °C) and warm temperature (20 °C to 26 °C) range samples separately because I had an overlapping treatment of 20 °C constant (with and without predators), leaving my two-way factorial design intact. To begin, I used a generalized linear model with negative binomial distribution (log-link, ‘glm.nb’ function in the *MASS* package) to determine how temperature, predators, and their interaction, affected prey abundance. I used a negative binomial distribution, as opposed to a Poisson distribution, because I had over-dispersed count data (i.e., the

variance of the data was greater than the mean). I then summarized my model using the ‘Anova’ function (in the *car* package) to calculate Type III Wald Chi-square statistics and P-values for my main and interacting terms. I followed a similar procedure for average prey body length, but here I used a generalized linear model with Gamma distribution (log-link, ‘glm’ function in base R) because prey body length data was positively, right-skewed. For all two-way ANOVAs, I performed a post hoc Tukey test for multiple comparisons if either the main effects or the interaction was significant (using the ‘lsmeans’ function in the *lsmeans* package) to determine which individual treatments were significantly different from one another.

Next, I analyzed if temperature affected predator abundance and average body length, along with PPMR using a one-way Analysis of Variance (ANOVA). I used ANOVAs instead of generalized linear models because in my preliminary data analysis I compared models to one another using Akaike information criterion (AIC) and found that the ANOVAs performed better than the generalized linear models (i.e., had lower AIC values). I removed a single replicate from my cool temperature range (specifically from 12 °C constant) as no predator individuals were extracted from that mesocosm in my predator body length and PPMR models. For all one-way ANOVAs, I performed a post hoc Tukey test if temperature treatment was significant. Finally, I used Kruskal-Wallis Rank Sum test to determine if temperature significantly affected predator-prey interaction strength, and subsequently a Dunn test for multiple comparisons (using the Bonferroni method) if temperature was statistically significant.

3.3 Results

After 40 days, I extracted and counted a total of 10,935 collembolan prey and 71 predator mite individuals from the cool temperature range mesocosms and 52,028 collembolan prey and 107 predator mite individuals from the warm temperature range mesocosms.

Within the cool temperature range experiment, I found that prey abundance was, on average, higher when prey was exposed longer to 20 °C when predators were absent (Figure 3-1A). However, both the inclusion of predators ($\chi^2 = 28.41$, $df = 1$, $P < 0.01$) and the interaction between predators and temperature ($\chi^2 = 12.00$, $df = 4$, $P = 0.02$)

significantly affected prey abundance, as abundances sharply declined and never exceeded 269 individuals when predator mites were present. Notably, prey abundance was considerably higher in the warm temperature range experiment (Figure 3-1C); when predators were absent, average prey abundance approached 3000 individuals (per mesocosm), but abundances were reduced by half when prey were mostly or only exposed to 26 °C ($\chi^2 = 13.36$, $df = 4$, $P = 0.01$). When predators were added, prey abundances were significantly lower across all temperature treatments ($\chi^2 = 93.44$, $df = 1$, $P < 0.001$), as average prey abundances were 4 to 10× lower with the addition of predators. Although the interaction between predators and temperature was not statistically significant ($\chi^2 = 3.38$, $df = 4$, $P = 0.50$), prey abundance in the 2:2 temperature treatment (when prey was evenly exposed to 20 °C and 26 °C) was more similar to the 20 °C constant treatment when there were no predators, but 26 °C constant treatment when predators were added.

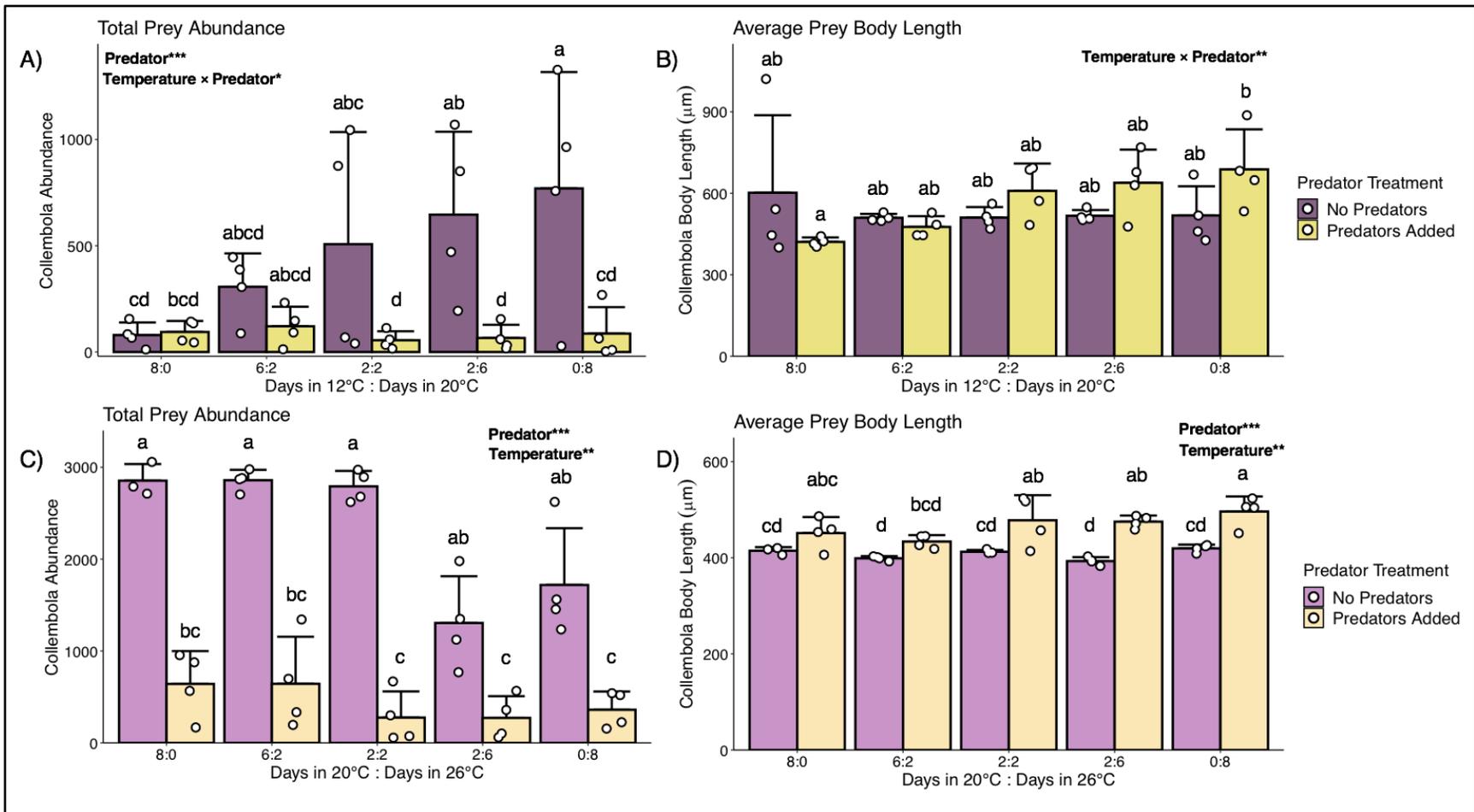


Figure 3-1 Total collembolan prey abundance (A and C) and average body length (B and D) in the cool (12 °C to 20 °C, A and B) and warm temperature range (20 °C to 26 °C, C and D).

Bars and error bars represent mean (\pm SD), and points are the raw data values. Significant treatment effects are presented in bold. * = $P < 0.05$, ** = $P < 0.01$, * = $P < 0.001$. Letters indicate significant differences ($P < 0.05$) between individual treatments, calculating using post hoc Tukey tests.**

I found a significant interaction between predators and temperature on prey body length in the cool temperature range ($\chi^2 = 14.03$, $df = 4$, $P = 0.007$). When predators were present the average body length of prey increased with greater exposure to 20 °C (Figure 3-1B). Yet, the average body length of prey was similar across the temperature treatments (excluding one mesocosm in the 12 °C constant treatment) when predators were absent. Changes to prey body length was more evident in the body length distributions. When predators were added and prey individuals were exposed exclusively or mainly to 12 °C (8:0, 6:2 temperature treatments; Figure 3-2A-B) the body length distribution shifted to the left, as body length became more concentrated towards smaller-bodied individuals (roughly 300-500 μm in length). However, when predators were added and prey were exposed evenly to, mainly to, or exclusively to 20 °C (2:2, 2:6, 0:8 temperature treatments; Figure 3-2C-E), prey body length distribution shifted to the right, indicating that the proportion of larger-bodied individuals increased within mesocosms. Similarly, predators increased the average body length of prey across all temperature treatments in the warm temperature range ($\chi^2 = 70.00$, $df = 1$, $P < 0.001$; Figure 3-1D), as small (at times less than 50 μm) but significant differences in average prey length was detected between the temperature treatments ($\chi^2 = 15.14$, $df = 4$, $P = 0.004$). Similar to the cool temperature range, I observed that the concentration of small-bodied collembolans (roughly 300-500 μm in length) within mesocosms had decreased when predators were added, providing further evidence that predators manipulated the body size distribution of their prey, as a function of temperature (Figure 3-3A-E).

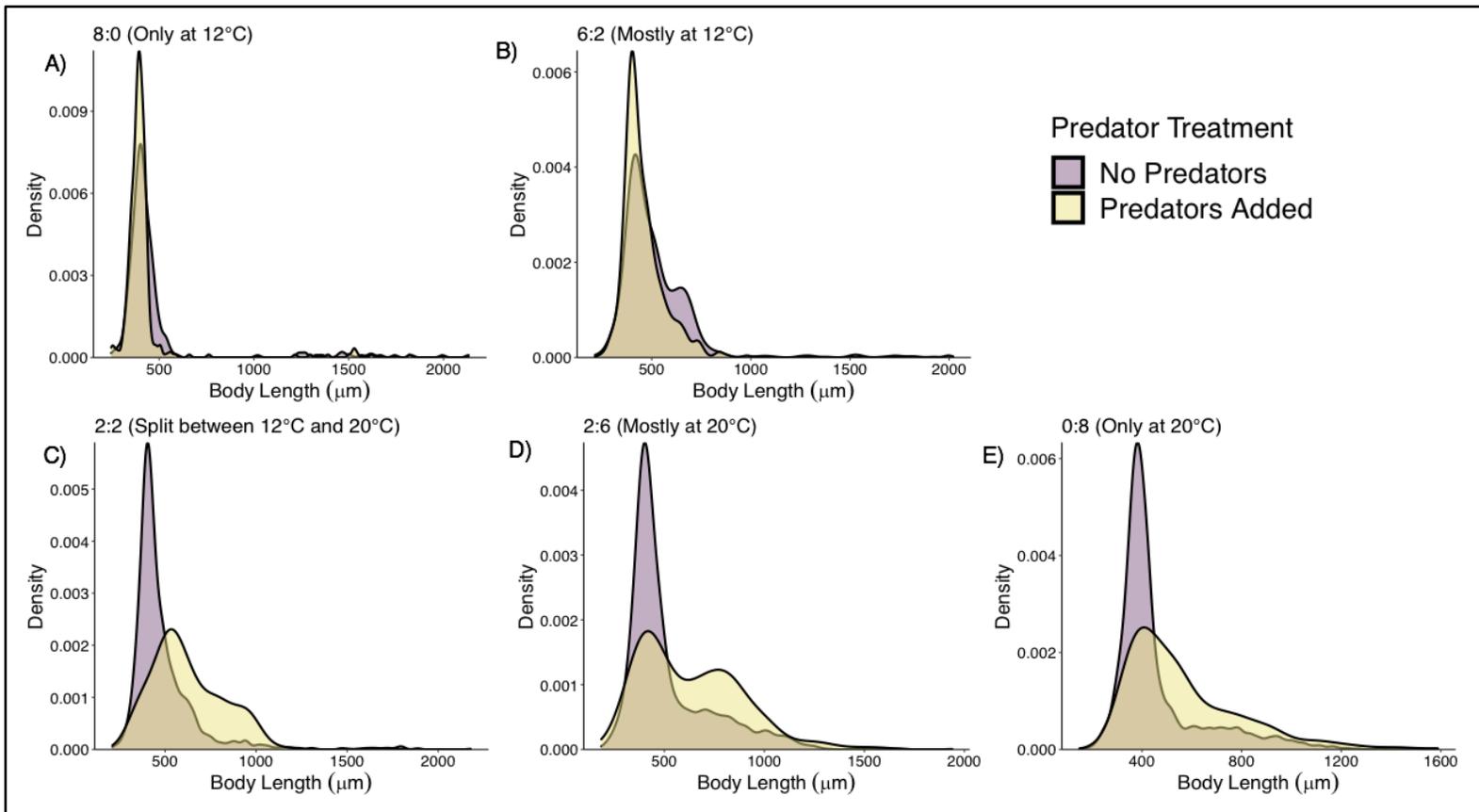


Figure 3-2 Density plots of prey body length in the cool temperature range (12 °C to 20 °C).

A) Prey body lengths at 12 °C constant (8:0), B) 6-days at 12 °C : 2-days at 20 °C (6:2), C) 2-days at 12 °C : 2-days at 20 °C (2:2), D) 2-days at 12 °C : 6-days at 20 °C, and E) 20 °C constant (0:8).

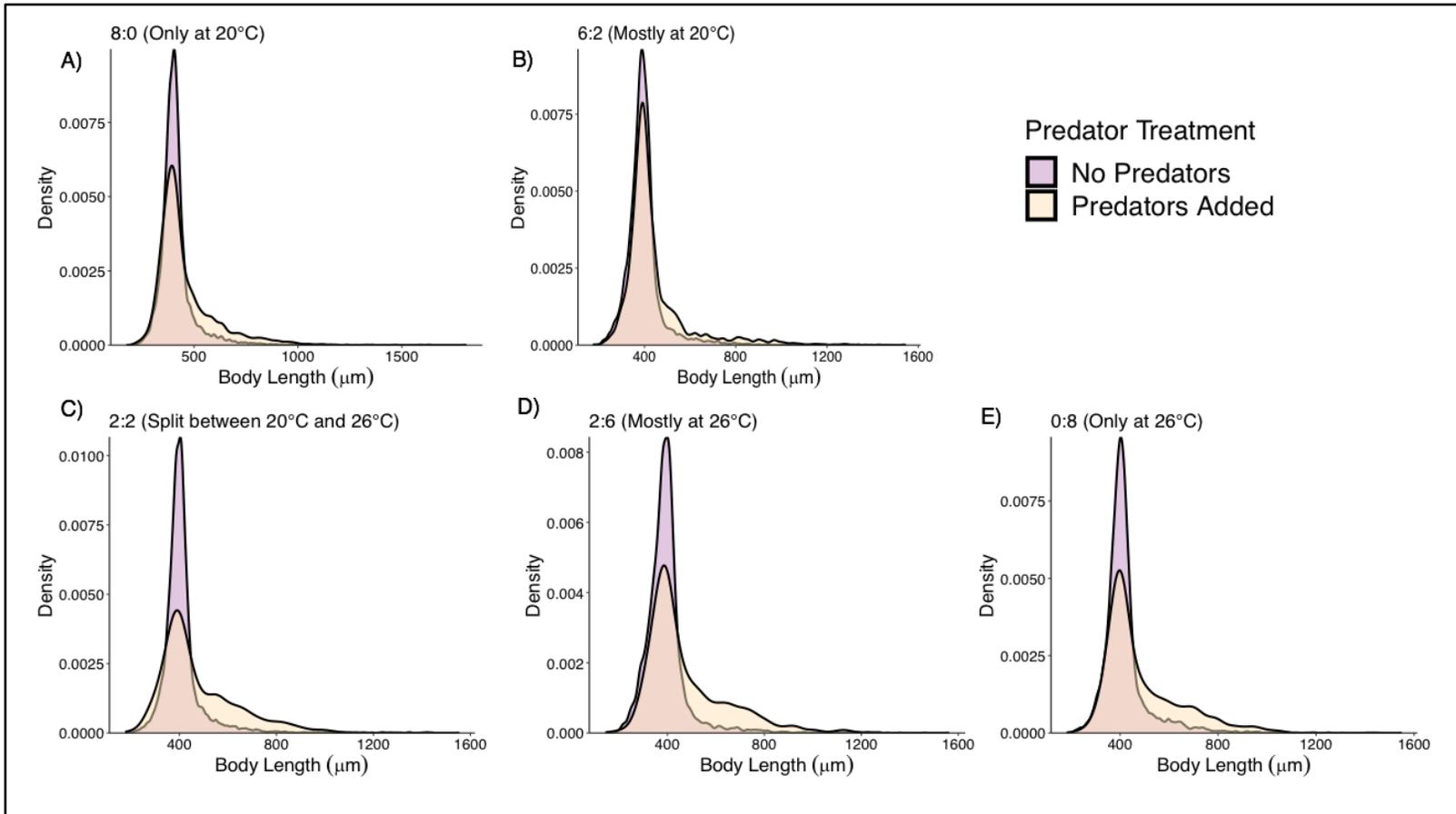


Figure 3-3 Density plots of prey body length in the warm temperature range (20 °C to 26 °C).

A) Prey body lengths at 20 °C constant (8:0), B) 6-days at 20 °C : 2-days at 26 °C (6:2), C) 2-days at 20 °C : 2-days at 26 °C (2:2), D) 2-days at 20 °C : 6-days at 26 °C, and E) 26 °C constant (0:8).

Despite significant changes to prey abundance within both temperature ranges, I found that predator abundance was not significantly affected by temperature (Figure 3-4A and C). The number of predator individuals often did not exceed the start of the experiment (i.e., five individuals), with abundance topping out at eleven individuals. Interestingly, I observed only adult predators, and not juvenile predators, in multiple temperature treatments. Juvenile individuals were only found in the 20 °C constant (in both the cool and warm temperature range), and in all other temperature treatments in the warm temperature range except 26 °C constant. In addition, predator abundance decreased in the warm temperature range in a stepwise fashion with greater exposure to 26 °C. The presence of juveniles had an observable effect on average predator body length (but was only statistically significant in the warm temperature range; $F_{4,15} = 3.07$, $P = 0.049$). Average predator body length became lower and more variable when juvenile individuals were found within populations (Figure 3-4B and D).

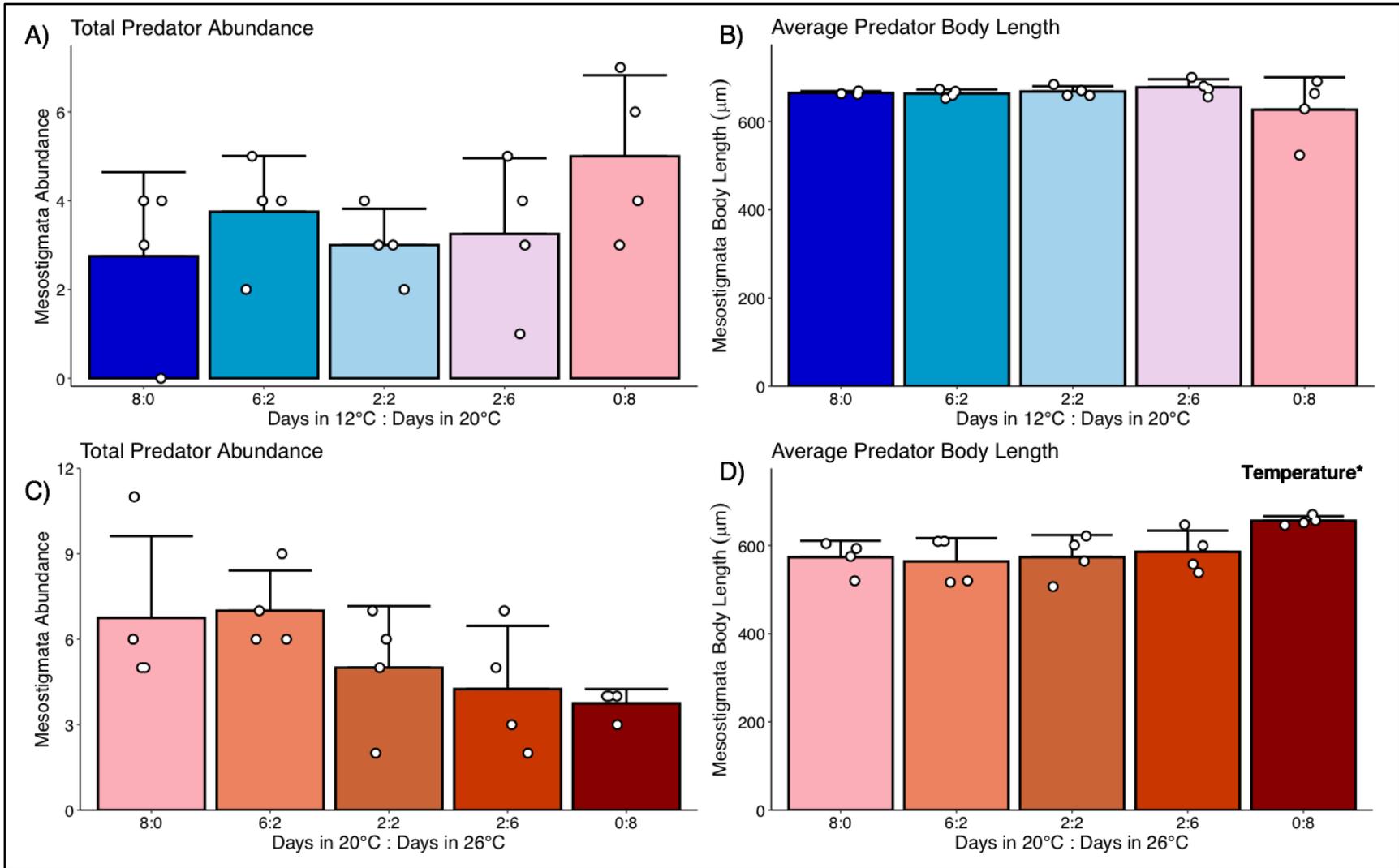


Figure 3-4 Total predator mite abundance (A and C) and average body length (B and D) in the cool (12 °C to 20 °C, A and B) and warm temperature range (20 °C to 26 °C, C and D).

Bars and error bars represent mean (\pm SD), and points are the raw data values. Significant treatment effects are presented in bold. * = $P < 0.05$.

Both PPMR and predator-prey interactions strength were significantly affected by temperature in the cool temperature range, but not the warm temperature range. In the cool temperature range, the difference between predator and prey body mass decreased with more exposure to 20 °C ($F_{4,14} = 4.52$, $P = 0.01$; Figure 3-5A), meaning predators and prey became more similar in size. Furthermore, predator-prey interaction strength was stronger when predators were exposed to 20 °C for any length of time (Kruskal Wallis test: $H = 11.39$, $df = 4$, $P = 0.02$; Figure 3-5B). At 12 °C constant, predators did not lower prey abundances, relative to when predators were absent, but exposure to 20 °C significantly increased predator-prey interaction strength. In the warm temperature range, PPMR was similar across the temperature treatments (Figure 3-5C) but predator-prey interaction strength was strongest in the 2:2 temperature treatment (when predators and prey were evenly exposed to 20 °C and 26 °C), although this was not statistically significant (Kruskal Wallis test: $H = 7.21$, $df = 4$, $P = 0.12$; Figure 3-5D).

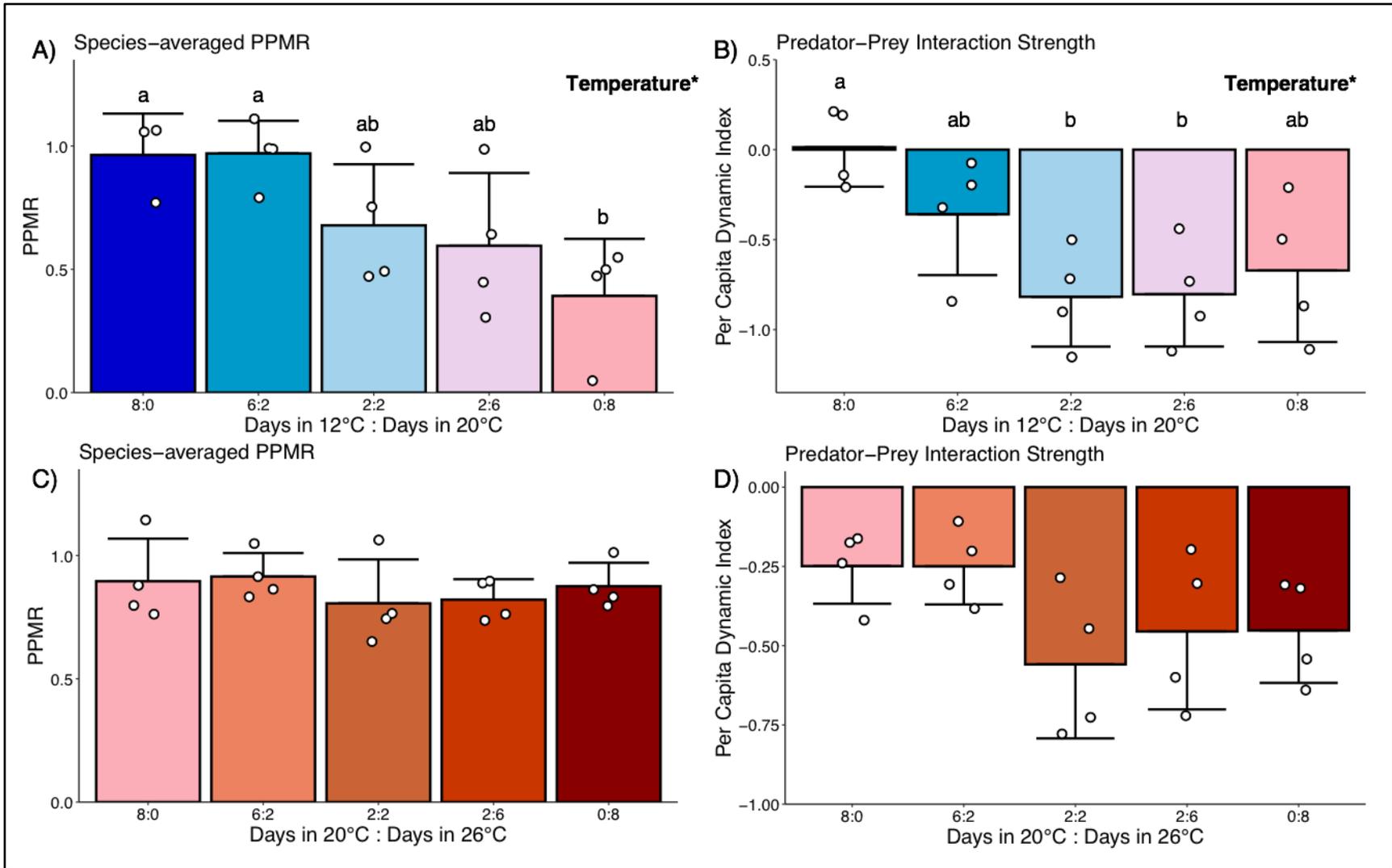


Figure 3-5 Predator-prey mass ratio (PPMR) (A and C) and interaction strength (Dynamic Index) (B and D) in the cool (12 °C to 20 °C; A and B) and warm temperature range (20 °C to 26 °C; C and D).

Bars and error bars represent mean (\pm SD), and points are the raw data values. Significant treatment effects are presented in bold. * = $P < 0.05$. Letters indicate significant differences ($P < 0.05$) between the temperature treatments, calculating using post hoc Tukey tests (for PPMR) or corrected using the Bonferroni method (for interaction strength).

3.4 Discussion

I experimentally tested how increasing mean and variability of temperature manifests in ectothermic predator-prey interactions at the population-level across a cool (12 °C to 20 °C) and warm (20 °C to 26 °C) temperature range. Under cooler temperatures, I found that prey (*F. candida*) abundances increased with more exposure to 20 °C (when no predators were added). But under warmer temperatures, prey abundances were high and unchanged until a ‘tipping point’ where increased exposure to 26 °C reduced prey abundance by half as population size responded strongly to temperature changes. Predators (*S. scimitus*) consistently lowered prey abundances, leading to strong predator-prey interactions, and shifted the body size distribution as the inclusion of predators typically increased average prey body length. Surprisingly, predator abundances were not affected by temperature as final abundances were often not higher than the starting abundance of five individuals.

3.4.1 Predator-prey interactions and prey populations

Ectotherm community body size distribution has shown to shift towards smaller-bodied individuals at higher temperatures (Daufresne et al., 2009; Dossena et al., 2012; Lindo, 2015; Yvon-Durocher et al., 2011), a phenomena known as ‘community downsizing’ (Sheridan and Bickford, 2011), partly due to the competitive advantage smaller individuals have over larger individuals at higher temperatures (Ohlberger et al., 2011; Reuman et al., 2014). But, because predation is also temperature sensitive (Dell et al., 2014, 2011; Gilbert et al., 2014) changing feeding behaviour and rate by predators may offset any competitive advantage that small-bodied individuals have as predators can increasingly feed on small-bodied individuals under warmer temperatures (Dobashi et al., 2018; Frances and McCauley, 2018; and Chapter 2 of this thesis). Within both temperature ranges, predators directly and/or indirectly increased the average body length (and mass) of prey when present, which has also been previously reported (Yvon-Durocher et al., 2015). Notably, warming is also predicted to decrease individual body size for ectotherms (Atkinson, 1994; Gardner et al., 2011), as faster growth rates for

individual leads to smaller adult body size. I found that the maximum prey body length was ~2000 μm at cooler temperatures, but only ~1600 μm under warmer temperatures, aligning with the temperature-size rule (Atkinson, 1994). Nevertheless, the consequence of increased average prey body size under warming means individual metabolic demands are greater, compared to their smaller counterparts (Brown et al., 2004; Gillooly et al., 2001). Although prey population metabolic rate (i.e., the total metabolic demand within prey populations) likely decreased – because of the smaller population size – the energy balance within the system has shifted as a result of predation.

Along with prey body length, predator-prey interaction strength was also affected by temperature. Predator-prey (or consumer-resource) interaction strength can increase when predators feed at higher temperatures (O'Connor, 2009). But higher prey development and population growth rates under warming can weaken interaction strength long-term if prey development and growth exceeds predator feeding rates (Davidson et al., 2021; Rall et al., 2010). I found that predator-prey interaction increased with greater exposure to 20 °C in the cool temperature range and was comparable across all treatments in the warm temperature change, indicating that this did not occur. But interestingly, predators lowered prey populations to similar sizes, regardless of temperature (about 100 and 450 individuals in the cool and warm temperature ranges, respectively). This was also observed by Thakur et al. (2018) who similarly used predator mite and collembolan prey populations in three temperature regimes (12 °C – 15 °C, 17 °C – 20 °C, and 22°C – 25 °C). It appears predators may reduce prey abundances to an equilibrium, one that balances predator feeding rate with prey development and population growth. Whether this trend appears over longer timescales (more than 40 (this study) or 60 (Thakur et al., 2018) days) is unclear, but predators greatly reduced prey abundance in my study.

Acute and sudden exposure to extreme temperatures can hinder ectotherm performance. Ramachandran et al. (2021) found that when predator mites were transplanted +8 °C (from 16 °C to 24 °C), feeding rates on small, soft-bodied *Carpoglyphus lactis* were significantly lower than predators already acclimated to 24 °C. This occurs because ectotherms require time to fully acclimate to warmer temperatures (Healy and Schulte, 2012; Pintor et al., 2016; Sandblom et al., 2014), as performance can improve with sufficient exposure (Ramachandran et al., 2021). Yet in my study,

collembolan prey was not particularly hampered by the sudden exposure to 26 °C (in the 2:2 temperature treatment within the warm temperature range) as average population size was similar to 20 °C constant. Instead, prey population size was reduced by half when collembolans were either mostly or constantly exposed to 26 °C (the 2:6 and 0:8 temperature treatments). Because of the experimental design I cannot determine the average temperature that leads to the decline of prey population size. But it appears that chronic exposure to an extreme temperature (26 °C) beyond T_{opt} was more detrimental to prey than acute exposure, suggesting that rising mean temperature impacted *F. candida* populations more than temperature variability.

3.4.2 Predator populations

Predator abundances hardly increased over the course of these experiments and did not respond to rising mean and temperature variability. This is surprising considering that *S. scimitus*, unlike their prey *F. candida*, purportedly thrive in warmer temperatures (+20 °C). *Stratiolaelaps scimitus* can reproduce 30 to 50 eggs during adulthood at 20, 25, and even 30 °C, with T_{opt} considered to be near 25 °C (Ydergaard et al., 1997). But *S. scimitus* juveniles were only present in a select number of temperature treatments. Juveniles were found in the 20 °C constant (in both the cool and warm temperature range), and 2:6, 2:2, and 6:2 treatments in the warm temperature range, but not at 26 °C constant temperature. The combination of two complementary mechanisms may explain the lack of predator population growth and juvenile presence in both temperature ranges. First, in the cool temperature treatment, exposure to 12 °C for any length of time likely stymied predator reproduction. For instance, Ydergaard et al. (1997) found that egg production of *S. scimitus* cultured at 15 °C was nearly 2× lower than 25 °C as females produced less than one egg per day. In addition, they also observed that egg and juvenile mortality was high (~17% on average) across four developmental stages (egg, larva, protonymph and deutonymph) at 15 °C. Possibly, low egg production paired with high juvenile mortality limited predator population growth at cooler temperatures. Conversely, increasing metabolic rate at 26 °C might have limited predator reproductive output. I estimated that predator metabolic demands were 1.26× at 26 °C vs. predators at

20 °C (and nearly doubled that of predators at 12 °C) (Appendix B; Table 1B). This small, but significant, increase in metabolic demands possibly hindered predator populations because less energy was available for reproduction.

The second mechanism to explain lack of predator reproduction relates to the feeding mode of *S. scimitus*. I estimated that an individual predator's consumption rate was 22, 34, and 43 prey individuals (40 days⁻¹) at 12 °C, 20 °C, 26 °C, respectively (Appendix B; Table 1B). This equates to roughly 100-200 prey needed to sustain starting predator populations over the course of the experiment. Many mesocosms (particularly in the warm temperature range) contained prey abundances that exceeded this minimum, so why did predator abundances remain low? While past studies have shown *S. scimitus* to have a high reproductive output under high temperatures, it is possibly this can be partly attributed to experimental design. In Ydergaard et al. (1997), predators were fed prey *ad libitum* and were maintained in small areas (height: 4 cm, diameter: 3 cm). In addition, Jensen et al. (2019) found that the predator mite species *Gaeolaelaps aculeifer* laid one egg for every *F. candida* killed at 20 °C when predators were maintained in individual well plates and were provided unlimited *F. candida*. In both these experiments, time spent foraging for predator mites was greatly reduced due to the small, homogenous arena such that prey was available on demand, meaning less energy was expended foraging and could be directed towards reproduction. In my experiment, predators needed to actively forage in a larger heterogenous habitat (due to the vermiculite) to capture and feed on prey, which increased foraging costs and reduced the available energy for reproduction. So, although *F. candida* reproductive output responded significantly with temperature, foraging costs paired with high juvenile mortality and low egg production (in the cold temperature range) or high metabolic demands (in the warm temperature range) likely limited *S. scimitus* reproduction in my experiment.

3.4.3 Conclusions

Climate change will transform ectotherm populations and communities, yet we know little how combined increasing temperature mean and variability will reshape

predation and predator-prey interactions. I observed stronger effects of temperature on the collembolan prey populations, rather than the predator mite populations, but this can partly be attributed to *S. scimitus* subsisting at higher temperatures than *F. candida* as predators did not respond to increased mean and temperature variability. Prey population size changed immensely with temperature. In the cool temperature range, increasing temperature mean and variability led to a step wise increase in prey abundance. But in the warm temperature range, prey abundances remained high, even with the sudden exposure to 26 °C (in the 2:2 temperature treatment) as populations only dropped when prey were mostly or entirely exposed to 26 °C (the 2:6 and 0:8 temperature treatments). This suggested that in the warm temperature range, that increasing average temperature and not temperature variability impacted prey populations more. Yet, the cumulative effect of predation on prey was consistent, as predators greatly reduced prey abundances and increased their average body length as differences in trends only stemmed from the constant or predominant exposure to 12 °C (8:0 and 6:2 temperature treatments in the cool temperature range). In the context of climate change, this suggests that species population size is more sensitive to climate change than species interactions. Correspondingly, the direct effects of climate change (changes to metabolic and physiological rates) impacted ectotherms more than the indirect effects (changes to species interactions). Teasing apart the direct and indirect effects of warming on ectotherm populations and communities is critical to better understand how on-going climate change will alter the natural world.

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Chapter 4

4 Short-term intensive warming shifts predator communities (Parasitiformes: Mesostigmata) in boreal forest soils¹

4.1 Introduction

Climate change represents one of the greatest threats to the natural world (Román-Palacios and Wiens, 2020). Already, global mean surface temperatures have risen nearly 1°C since the mid to late 19th century (IPCC, 2021), and are expected to increase further over the next century. This temperature increase will coincide with longer and more frequent short-term, extreme warming events (e.g., heat waves) that may last for several days and weeks (Meehl and Tebaldi, 2004; Viceto et al., 2019). A heat wave can broadly be defined as a period of at least three consecutive days of excessively hot weather (Perkins-Kirkpatrick and Gibson, 2017; Perkins and Alexander, 2013). Climate warming will increase both average seasonal temperatures and the frequency of heat waves at northern latitudes during the summer months (Bathiany et al., 2018; Price et al., 2013), thus ecosystems such as boreal forests will be greatly affected by climate warming. It is predicted that the annual mean temperature in the boreal forest will increase by 2° C by 2050, and possibly 4 – 5 °C by 2100 (Price et al., 2013) as the number of heat wave days will also increase in the boreal zone (Perkins-Kirkpatrick and Gibson, 2017). Increases to both average temperature and temperature variability will mean boreal forests will be under new temperature regime in the near future.

Soil systems of the boreal forest contain a rich organic layer that is habitat for hyperdiverse soil communities, where diversity is comparable, and can even exceed diversity in tropical forests (Coleman et al., 2018; Maraun et al., 2007). Boreal forest soils are populated mainly by microarthropods, such as mites (Arachnida: Acari) and

¹ Meehan, M.L., Caruso, T., Lindo, Z. 2021. Short-term intensive warming shifts predator communities (Parasitiformes: Mesostigmata) in Boreal forest soils. *Pedobiologia*. 87-88:150742.

collembolans (Hexapoda: Collembola), along with nematodes (Nematoda). Mites consists of two superorders, Acariformes and Parasitiformes, both of which are found in soil. This includes the fungi- and detritus-feeding Oribatida (Acariformes) (Norton and Behan-Pelletier, 2009), the highly derived Astigmata (Acariformes) (OConnor, 2009), and the trophically diverse Prostigmata (Acariformes) (Walter et al., 2009). Collembolans, commonly referred to as springtails, are soft-bodied hexapods that live within and atop soil (Coleman et al., 2018) and are generally considered fungi and detritus feeders (Chahartaghi et al., 2005). Nematodes are smaller than both mites and collembolans and live within the water films or water filled pore space (opposed to mites and collembolans that live within soil pore space; Coleman et al., 2018). Nematodes exhibit various feeding preferences and can be classified as bacteria feeders, fungi feeders, plant feeders, predators, and even omnivores (Bongers and Bongers, 1998; Yeates et al., 1993). Together, densities of microarthropods within soil habitats can exceed 800,000 individuals per m² (Behan et al., 1978), and 1,000,000 individuals per m² for nematodes (Petersen and Luxton, 1982), creating a highly connected food web with numerous feeding guilds and trophic levels (Hunt et al., 1987; Moore et al., 2003).

Another commonly found mite group in soils systems are mesostigmatic mites (Parasitiformes: Mesostigmata). Mesostigmatic mites are speciose group of mainly free-living, soil predators with about 11,000 described species (Walter and Proctor, 2013). In Canada, 650 described species across 46 families have been recorded, with over half of the families present within the boreal forest, producing diverse soil communities (Beaulieu et al., 2019; Meehan et al., 2018). As predators, mesostigmatic mites regulate the populations of their prey through top-down control and link the basal energy channels (i.e., fungi and bacteria) to one another (Hunt et al., 1987; Moore et al., 2003; Schneider and Maraun, 2009). Mesostigmatic species are also morphologically, physiologically, and functionally diverse. Mesostigmata body length can range from 200 µm – 4500 µm (Lindquist et al., 2009), as adult body mass is typically between 2 – 60 µg (Newton and Proctor, 2013). Mesostigmatic mites also exhibit various types of sexual systems as species can reproduce in multiple fashions (Norton et al., 1993) producing skewed male : female ratios for some species within communities (Błoszyk et al., 2004). Mesostigmata species can be diplodiploidy where offspring are reproduced sexually, and roughly equal

abundances of male and female individuals are present. As well, some Mesostigmata species reproduce asexually (parthenogenetically). Thelytokous parthenogenesis is often observed within Mesostigmata, whereby only females are reproduced producing all-female populations (Norton et al., 1993). Finally, mesostigmatic species also vary in feeding preferences (Beaulieu and Walter, 2007; Walter, 1988; Walter et al., 1988). Soil Mesostigmata species can often be broadly categorized as generalist arthropod and nematode feeders, or nematode-feeding specialists, with specialists having greater-top down control on their prey populations than generalists (Laakso and Setälä, 1999). Mesostigmatic generalist feeders can consume a wide variety of arthropod prey, including collembolans (Beaulieu and Walter, 2007; Schneider and Maraun, 2009), soft-bodied mites, along with juvenile Mesostigmata (Beaulieu and Walter, 2007; Walter, 1988; Walter et al., 1988).

Climate warming may impact soil communities through both direct and indirect mechanisms. Directly, warming will increase individual metabolic and population growth rate (Brown et al., 2004), leading to greater metabolic demands and higher total abundances (Jensen et al., 2018; Lindo, 2015). While indirectly, warming may alter soil communities through plant-soil feedbacks via changing plant detritus quality (i.e., C:N ratio of detritus) and rhizodeposits (i.e., quantity and composition of root exudates) (Pugnaire et al., 2019), along with decreasing soil moisture content (Holmstrup et al., 2017). As such, the effect of warming on soil faunal communities appears to vary temporally and/or be context dependent. Past studies have shown that soil fauna abundance, richness or diversity can increase or decrease under warming due to habitat differences (Bokhorst et al., 2008; Sjørnsen et al., 2005) and year-to-year fluctuations in climatic conditions (Harte et al., 1996; Meehan et al., 2020). This is because soil fauna respond strongly to changing abiotic and biotic environmental conditions induced by warming. For example, warming can decrease soil moisture or water content, resulting in lower soil fauna diversity and biomass (Holmstrup et al., 2017; Vestergård et al., 2015), because some soil taxa are prone to desiccation (Lindo et al., 2012). For predators, like mesostigmatic mites, increased prey abundances under warming may lead to greater predator abundances (Sjørnsen et al., 2005), as bottom-up mechanisms may affect predator persistence at higher temperatures.

Our understanding of soil faunal response to climate warming is also confounded by the duration of warming. Soil faunal response to continuous, long-term warming (5+ years) have shown to weakly affect communities (Alatalo et al., 2017; Holmstrup et al., 2017), whereas studies of short-term (that span weeks or months) or seasonal warming have shown to alter soil fauna composition (Bokhorst et al., 2012; Krab et al., 2013; Lindo, 2015; Markkula et al., 2019). Such short-term changes can be explained by species-level traits, like body size or sexual system. Long-term warming may allow for organisms to acclimate to warmer conditions and communities to reassemble, whereas short-term warming may induce immediate changes to community composition. Soil-dwelling species differ in their ability to acclimate to new temperature conditions (van Dooremalen et al., 2013) and in their response time to environmental change (Lindberg and Bengtsson, 2005). With increasing temperature variability and extreme warming events, the immediate response of fauna, whether it be positive or negative, will shift community structure.

The majority of climate warming studies on soil fauna have focused on collembolan and oribatid mite communities (Alatalo et al., 2017; Holmstrup et al., 2017; Lindo, 2015; Markkula et al., 2019; but see Meehan et al., 2020) without providing species-level information on how mesostigmatic mite communities respond. Mesostigmatic mites are essential contributors to soil functionality due to their high trophic position and providing top-down control on lower trophic levels (Hunt et al., 1987; Moore et al., 2003; Schneider and Maraun, 2009). Meaning, it is important to determine how rising temperatures will affect Mesostigmata assemblages, as changing community structure under warming may alter the strength of their top-down control on their prey (Laakso and Setälä, 1999). Here, I tested the effect of short-term (three months), intensive warming (+8 °C) with a focus on mesostigmatic mite assemblages from the boreal forest using experimental mesocosms. I used both a taxonomic as well as trait-based approach to examined how warming shifted mesostigmatic adult and juvenile abundance, species richness, diversity, evenness, assemblage composition, and community weighted mean (CWM) of body mass within Mesostigmata assemblages. As mesostigmatic mite persistence at higher temperatures may be dependent on prey availability, I enumerated other mite groups, along with collembolans and nematodes to

determine how warming affected their assemblages. The mesocosm approach also controls for any warming-induced indirect effects through plant-soil interactions or changes in soil moisture. If soil mesostigmatic assemblages respond to warming through metabolic and reproductive increases, and changes to prey availability, then total Mesostigmata abundances will increase, shifting community composition within mesocosms.

4.2 Methods and materials

4.2.1 Sampling site and experimental design

Forest-floor material for the mesocosms used in this study were collected from a boreal forest near White River, Ontario, Canada (48°21' N, 84°20' W). The forest contains a mixture of deciduous and coniferous tree species, consisting of white birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) B.S.P) (Webster and McLaughlin, 2010). The historic mean annual temperature and precipitation (1980 – 2007) for the study site is 2.1 °C and 980 mm, respectively (Webster and McLaughlin, 2010). From 1977 – 2014, the daily growing season temperature (May – September) for the area was 12.4 °C (Appendix C; Figure 1C). In October 2019, three contiguous forest-floor mats were collected measuring 34 cm × 21.7 cm × 13.2 cm. These mats were comprised of a mossy top layer containing mixed feather mosses mainly consisting of *Ptilium crista-castrensis* (Hedw.) and some *Pleurozium schreberi* (Brid.) Mitt., with a rich organic layer underneath, providing the habitat for the microarthropods and nematodes used in this study (Appendix C; Image 1C). Mats were shipped to Western University (London, Ontario, Canada) upon collection and stored at 4 °C until the beginning of the experiment.

After removing the living moss layer, I systematically divided the rich organic layer of the mats to create 24 experimental mesocosms. Both experimental treatments contained between three and five replicates from each mat, for a total of 12 replicates within each treatment. Each mesocosm consisted of ~155 g wet weight of organic material placed into a 500 mL mason jar. Jars were sealed but lids contained a 1 cm hole with a small piece of foam to allow for air flow during the experiment. I incubated mesocosms in complete darkness within environmental growth chambers at 12 °C or 20

°C, with 12 °C representing the average temperature over the growing season (May – September) at my collection site. As the boreal zone temperature may increase ~4 °C by 2100 (Price et al., 2013), I then simulated a ‘heat wave’ by adding an additional 4 °C (Perkins-Kirkpatrick and Lewis, 2020) to create my warming treatment of 20 °C (12 °C + 4 °C in annual mean temperature in the boreal forest by 2100, + 4 °C to simulate a heat wave = 20 °C). The length of treatment (three months) corresponds with the approximate length of the boreal forest growing season. Although a single heat wave would not last an entire growing season, there is an expected additional 10 – 20 heat wave days in the boreal zone for every 1 °C increase in global temperatures (Perkins-Kirkpatrick and Gibson, 2017), while the number of heat wave events, the length of heat waves, and the peak intensity of heat waves (i.e., the hottest day of the hottest event) will also increase, suggesting much of the boreal forest growing season will coincide with extreme warming events under future climatic conditions. Already, extended heat waves have been observed at northern latitudes with extreme monthly temperatures (+ 6 °C), well above the historical average (Overland and Wang, 2021).

I watered mesocosms weekly to maintain gravimetric soil moisture (i.e., amount of water per mass of wet soil) lost through evaporation and to minimize the indirect effects of warming on soil moisture in my study; each week I typically added 0.5 – 1 g of water to the 12 °C mesocosms, and 1 – 2 g to the 20 °C mesocosms. Mesocosms were incubated at their respective temperatures for three months (October 2019 – January 2020) whereafter I extracted microarthropods and nematodes.

4.2.2 Soil fauna sampling and identification

Subsamples (~60 g wet weight) from each mesocosm were placed on Tullgren funnels with 25-watt light bulbs for seven days to extract microarthropods into 75% EtOH. Tullgren funnels work by creating a desiccated gradient, driving soil microarthropods downwards, whereafter microarthropods fall and are collected in vials of EtOH. Also, I subsampled ~20 g wet weight from each mesocosm to extract nematodes using Baermann funnels over two days into water. Subsamples were wrapped in Kimwipes and submerged in a funnel filled with water, connected to a clamped rubber

tube. Nematodes are extracted by individuals swimming towards then sinking to the bottom of the clamped tube. After 48 hours, the rubber tube is unclamped and extraction fluid containing nematodes is collecting. Whereafter, nematodes are fixed in 4% formalin solution and stained with Rose Bengal, which darkens nematodes and become easier to count. Once microarthropods and nematodes were extracted, I counted the overall abundances (i.e., number of individuals in a mesocosm) of Oribatida, Astigmata and Prostigmata mites, along with Collembola and Nematoda individuals within each subsample. Further, I counted juvenile and adult Mesostigmata and identified adults to species/morphospecies-level (hereafter ‘species’) (Appendix C Table 1C). I used unpublished keys acquired from the Ohio State Acarology Summer Program (Mesostigmata Week, Summer 2016), along with published keys and papers for each family and genera (Emberson, 1967; Halašková, 1977, 1969; Hurlbutt, 1984, 1967, 1963; Marshall, 1964; Mašán, 2003; Petrova, 1967; Sikora, 2014). All abundances and mesostigmatic species richness (i.e., number of species in a mesocosm) were standardized by the absolute wet weight (in grams) of each subsample to account for any differences in subsample size for microarthropods and nematodes. For mesostigmatic assemblages, I calculated Shannon-Weiner diversity and Pielou’s evenness indices using the proportional abundances of each mesostigmatic species.

Shannon-Weiner diversity index (Shannon, 1948) was calculated for each mesocosm using the equation:

$$H' = -\sum(p_i) * (\ln(p_i)),$$

Where p_i is the relative proportion of each mesostigmatic species abundance. Pielou’s evenness (Pielou, 1975) was then calculated for each mesocosm using the equation:

$$J' = \frac{H'}{\ln(S)}$$

Where S is the unstandardized mesostigmatic species richness from each mesocosm.

4.2.3 Body mass calculations

I calculated the average adult body mass (μg) of each mesostigmatic species using length and weight measurements of up to 12 mites per species using the formula described in Persson and Lohm (1977):

$$W = 0.85 * (L^{2.09} * l^{0.84} * 10^{-6.44}),$$

where W is body mass in μg , L is the length of the idiosoma (body length, excluding mouthparts and legs) in μm , and l is the width of idiosoma in μm (Appendix C Table 1C). Length and width measurements were made on slide-mounted individuals with 40 \times , 100 \times , or 200 \times magnification (depending on the size of the mite) using calibrated Nikon NIS Element compound microscope (v.4.20.01) with imaging software. Slide-mounted mesostigmatic individuals may have flattened, increasing the length and width of their idiosoma. However, because mesostigmatic mites generally have a flat dorsal-lateral shape (as opposed to some Oribatida species) slide-mounting likely had little impact on the length and width measurements. The body mass for each species was used to calculate a Community Weighted Mean (CWM) value of body mass for the Mesostigmata assemblages. The CWM considers the average body mass for each species weighted by the proportional abundance of each species using the equation:

$$\text{CWM body mass} = \sum (p_i \times x_i),$$

Where p_i is the proportional abundance of species i and x_i is the average adult body mass calculated from length and width measurements.

4.2.4 Statistical analysis

I performed all statistical analyses using the R statistical program (R Version 3.5.1; R Core Team, 2018). For all statistical tests, I evaluated the underlying assumptions of each model. To analyze the effect of warming on Mesostigmata species richness, Shannon diversity index, Pielou's evenness, and Oribatida, Astigmata, Prostigmata, Collembola and Nematoda abundance, I used Type II Sums of Squares ANOVAs (Analysis of Variance) with temperature and mat number as the independent variables within the models. Mat number (1, 2 and 3) was included as a nominal additive term within all my models to account for variation between mats. I used Type II ANOVAs (and subsequent MANOVAs (Multivariate Analysis of Variance), see below) because these two independent variables had no interactive term, and to accommodate the

unbalanced design between mat number and temperature treatments using the ‘Anova’ function in the *car* package which calculated F-statistics and P-values.

Similarly, I used a Type II MANOVA to test how warming impacted adult and juvenile mesostigmatic abundance with temperature and mat number as the independent variables. I used a MANOVA instead of an ANOVA for the initial test as adult and juvenile abundances are likely not independent of one another. I then ran separate Type II ANOVAs as post hoc tests to determine whether adults and juveniles separately were affected by warming. In addition, I tested how warming affected the proportion of juveniles within mesostigmatic assemblages using a logistic regression with quasi-binomial distribution (Zuur et al., 2009). Logistic regressions are used when data is either proportional or presence/absence and are typically analyzed assuming a binomial distribution. However, my data was under-dispersed, meaning there was less variability in my data than predicted with a binomial distribution. Therefore, I corrected for this using a quasi-binomial distribution. Afterwards, I used a Type II ANOVA to summarize my model to calculate Wald Chi-square statistics and P-values (Wald Chi-square statistics because I used a generalized linear model as opposed to a linear model) to determine the significance of temperature on the proportion of juveniles within Mesostigmata assemblages.

I calculated the community weighted means (CWM) for mesostigmatic mite species body mass using the *FD* package's ‘dbFD’ function to test how warming affected the average individual body mass within Mesostigmata assemblages. I calculated only adult CWM body mass because I did not identify mesostigmatic juveniles to species-level. I used a Type II ANOVA with temperature and mat number as the independent variables and CWM of body mass as the dependent variable within my model.

Finally, I tested whether warming and the abundances of potential prey groups (Oribatida, Astigmata, Prostigmata, Collembola and Nematoda) affected adult Mesostigmata assemblages using a distance-based Redundancy Analysis (db-RDA, with Bray-Curtis dissimilarity) with the ‘capscale’ function in *vegan* package. A db-RDA is a type of ordination analysis that summarizes multivariate data (data with more than one dependent variables) onto a reduced number of axes (typically two) (Borcard et al., 2011). A db-RDA is considered a constrained ordination, where the multivariate dataset

of independent variables (i.e., warming treatment and prey abundances) is compared with another multivariate dataset of dependent variables (i.e., Mesostigmata assemblage) to test for significant relationships between the two matrices (Borcard et al., 2011). Dissimilarity matrices (e.g., Euclidean, Bray-Curtis) are typically employed in ordinations to compute pairwise comparisons between elements dependent variables (i.e., pairwise comparisons between mite communities). I used a Bray-Curtis dissimilarity matrix for the Mesostigmata communities because the dataset was populated with many zeroes. I assessed for collinearity (i.e., if two or more independent variables are correlated with each other) in my initial model using variance inflation factor (VIF) scores, where scores <10 represented acceptable collinearity (Zuur et al., 2007). Starting with the initial model (warming, mat number and potential prey group abundances), I used the ‘ordistep’ function in the *vegan* package to perform backwards selections to determine the explanatory factors that explain Mesostigmata assemblage composition. Backwards selections assess the initial model containing all explanatory terms, then removes a single term with each step until the top model is reached, determined by permutation tests. Once the top model was reached, I reported the marginal effect (i.e., the effect of an explanatory variable when all other terms are present in the model) of each explanatory factor.

4.3 Results

After three months of incubation at 12 °C and 20 °C, I counted 3,349 individuals (1,899 adults and 1,450 juveniles) and identified 14 Mesostigmata species within my study, with an average of 139.54 ± 89.57 (mean \pm SD) individuals, and 7.00 ± 1.18 species across my 24 mesocosms. By and large, the most species rich and abundant Mesostigmata family across both treatments was the nematode-feeding Zerconidae (Appendix C; Table 1C). Further, I counted 6,648 individuals of Oribatida (277.00 ± 174.44 individuals per mesocosm), 5,484 individuals of Astigmata (228.50 ± 263.86 individuals per mesocosm), 560 individuals of Prostigmata (23.33 ± 21.31 individuals per mesocosm), 3,541 individuals of Collembola (147.54 ± 114.90 individuals per mesocosm), and 24,080 individuals of Nematoda (1003.33 ± 550.43 individuals per mesocosm), for a total of 43,662 individuals within my study.

Three months of warming did not significantly alter the species richness, diversity, or evenness in mesostigmatic mite assemblages (Table 4-1). In addition, there was no significant difference in either the overall abundances of oribatid mites, collembolans, or nematodes in my 12 °C and 20 °C treatments (Table 4-2).

Table 4-1 Mesostigmata species richness, diversity and evenness within 12 °C and 20 °C assemblages.

Results from Type II ANOVAs that tested for the effect of warming on mesostigmatic community indices are provided. Indices are reported as mean (\pm SD) at 12 °C and 20 °C based on unstandardized richness and standardized abundance data for diversity and evenness. Note, I analyzed richness standardized (by gram wet weight of organic matter) but are showing unstandardized richness for ease of interpretation.

Community Indices	12 °C	20 °C	F _{1,20}	P-value
Species richness	6.83 (1.27)	7.17 (1.11)	0.07	0.801
Shannon-Weiner diversity index	1.36 (0.29)	1.42 (0.19)	0.60	0.446
Pielou's evenness	0.71 (0.11)	0.72 (0.07)	0.50	0.490

Table 4-2 Abundance (number of individuals per gram wet weight) of the major microarthropod taxa (excluding Mesostigmata) and nematodes within 12 °C and 20 °C mesocosms.

Results from Type II ANOVAs that tested for the effect of warming on abundances are provided. Bold text represents significant results ($P < 0.05$). Abundances are standardized (by wet weight of organic material) and are reported as mean abundance (\pm SD) at 12 °C and 20 °C.

Higher Taxon Group	Lower Taxon Group	12 °C	20 °C	F _{1,20}	P-value
Acari	Oribatida	4.87 (2.87)	4.71 (3.27)	0.13	0.727
Acari	Astigmata	1.01 (1.06)	6.78 (4.68)	16.26	< 0.001
Acari	Prostigmata	0.54 (0.36)	0.27 (0.34)	6.01	0.024
Hexapoda	Collembola	2.30 (1.39)	2.81 (2.52)	0.36	0.556
Nematoda		53.18 (27.77)	39.44 (20.69)	2.68	0.117

However, warming did significantly affect the overall abundances of two other major mite groups, as astigmatic mite abundances were 6× greater within 20 °C mesocosms ($F_{1,20} = 16.26$, $P < 0.001$), while prostigmatic mite abundance was lowered by half at 20 °C, compared to 12 °C ($F_{1,20} = 6.01$, $P = 0.024$; Table 4-2). In addition, total mesostigmatic abundance was significantly greater at 20 °C, compared to 12 °C (Pillai test statistic = 0.54, $F_{2,19} = 11.26$, $P < 0.001$; Figure 4-1), as both adult ($F_{1,20} = 10.79$, $P = 0.004$) and juvenile ($F_{1,20} = 23.56$, $P < 0.001$) abundances were higher under warming. This shifted the assemblage age structure of Mesostigmata toward juveniles (Wald $\chi^2 = 18.32$, $df = 1$, $P < 0.001$), as the proportion of juveniles within assemblage doubled at 20 °C. Further, I found that community-level individual body mass (i.e., weighted average across all species) of Mesostigmata ($F_{1,20} = 18.83$, $P < 0.001$; Figure 4-2) was also greater at 20 °C, as the average mesostigmatic individual was ~4 μg (1.4×) heavier at 20 °C, compared to 12 °C (Appendix C; Table 1C).

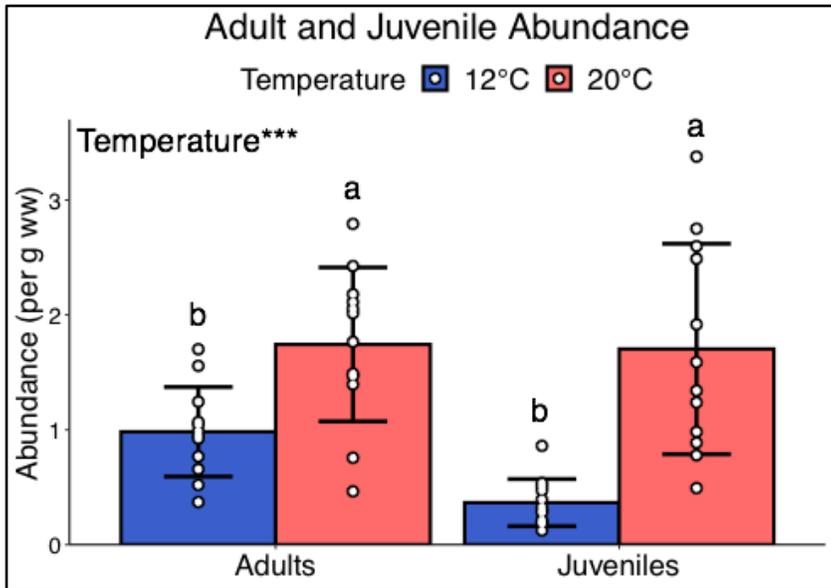


Figure 4-1 Mesostigmata adult and juvenile abundances within 12 °C and 20 °C mesocosms.

Bars are mean \pm SD, while points are data values for each treatment, per g ww = per gram wet weight of organic material. Temperature significantly affected mesostigmatic adult and juvenile abundances, * = $P < 0.001$. Letters denote significant differences ($P < 0.05$) from post hoc tests for adult and juvenile abundance.**

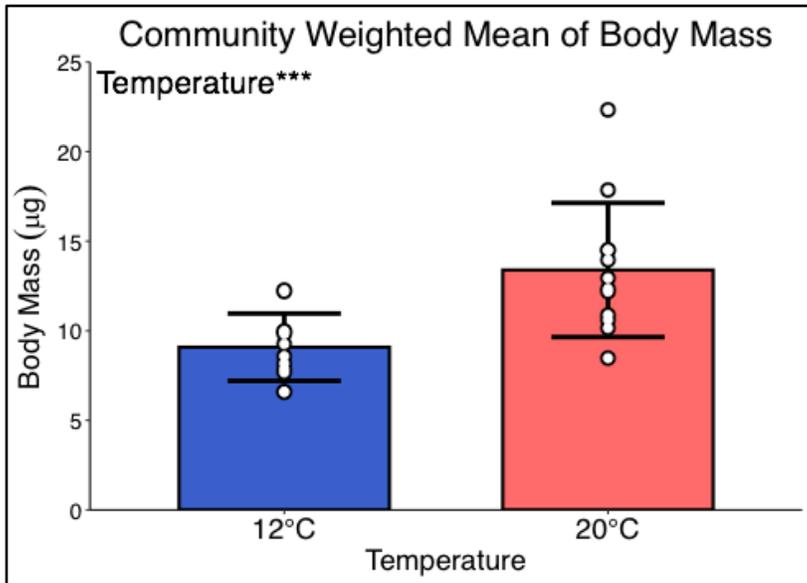


Figure 4-2 The community weighted mean (CWM) of body mass for an adult Mesostigmata within 12 °C and 20 °C mesocosms.

Bars are mean \pm SD, while points are data values for each treatment. Temperature significantly affected mesostigmatic community-level body mass, *** = $P < 0.001$.

The top model that explained Mesostigmata assemblage consisted of temperature ($F_{1,17} = 2.77$, $P = 0.002$), mat number ($F_{2,17} = 1.61$, $P = 0.02$), along with the overall abundances of Astigmata ($F_{1,17} = 1.55$ $P = 0.08$), Prostigmata ($F_{1,17} = 1.81$ $P = 0.03$), and Collembola ($F_{1,17} = 2.01$ $P = 0.02$) (Figure 4-3). Although species richness, diversity, or evenness did not differ between 12 °C and 20 °C assemblages of Mesostigmata, the abundances of Mesostigmata species changed, shifting assemblage composition at 20 °C. I found *Veigaia mitis* (Berlese) and *Asca garmani* Hurlbutt were 8.7× and 2.5× more abundant at 20 °C, compared to 12 °C. Similarly, I also found that *Zercon* nr. *carolinensis* Halašková and *Dinychus* sp.1 abundances were 2.5× and 4× greater at 20 °C. Not all species benefited from warming however as *Caurozercon duplex* Halašková abundance was lowered by half at 20 °C, compared to 12 °C, whereas the most abundant species in my study, *Parazercon radiatus* Berlese, had similar abundances at both 12 °C and 20° C.

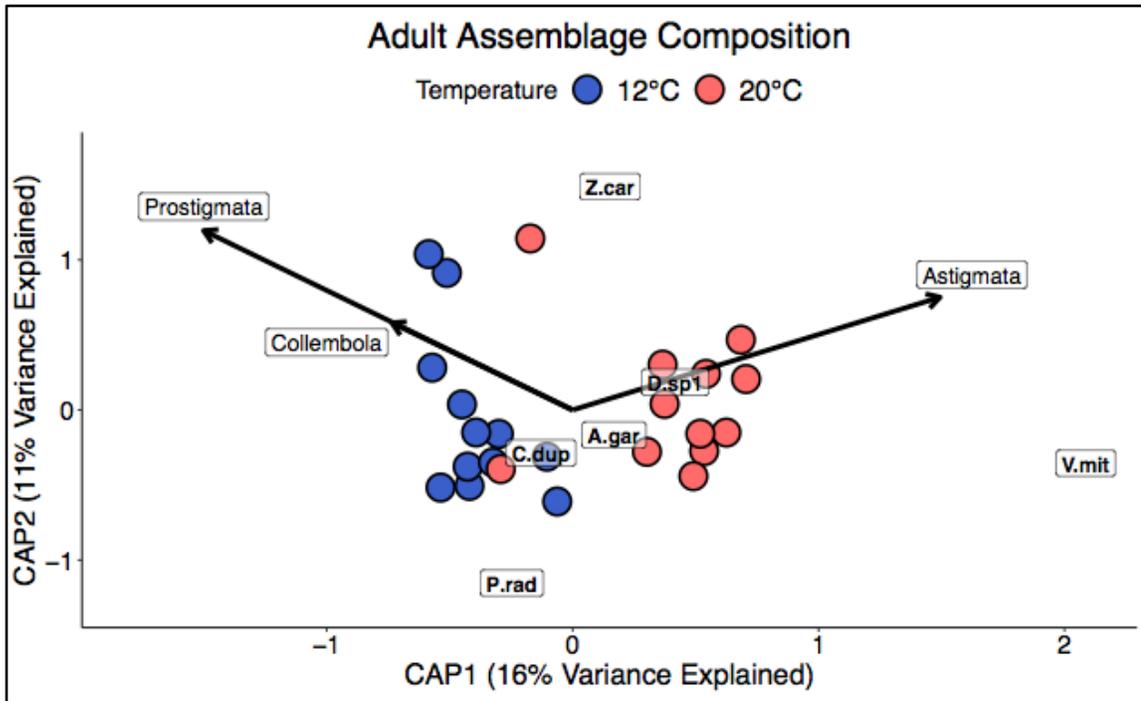


Figure 4-3 Distance-based Redundancy analysis (db-RDA; with Bray-Curtis dissimilarity) of adult Mesostigmata assemblages within 12 °C and 20 °C mesocosms.

Plotted in bold are the six species with the largest axis loadings. *A.gar* = *Asca garmani*, *C.dup* = *Caurozercon duplex*, *D.sp1* = *Dinychus sp.1*, *P.rad* = *Parazercon radiatus*, *V.mit* = *Veigaia mitis*, and *Z.car* = *Zercon nr. carolinensis*. Temperature significantly affected Mesostigmata communities ($P = 0.002$); biplot arrows represent prey group abundances (Astigmata, Prostigmata, and Collembola) that correlated with mesostigmatic mite communities, while individual points are experimental mesocosms.

4.4 Discussion

In this study, I tested the effect of short-term, intensive warming on soil Mesostigmata assemblages from a boreal forest. I found that +8 °C of warming did not impact Mesostigmata species richness, diversity, or evenness, but warming increased both adult and juvenile abundances significantly, as species such as *Asca garmani* and *Veigaia mitis* had greater abundances at 20 °C, leading to a significantly different assemblage composition under warming. The greater abundances of *V. mitis*, a medium-sized predator, corresponded with a higher average body mass for a Mesostigmata individual at 20 °C. Changes in the soil food web in boreal forest soils, especially among the most abundant predators, may have cascading consequences on the movement of energy and nutrients through the soil food web. Meaning, that rising global temperatures and increased frequency of short-term, extreme warming events (e.g., heat waves) (Meehl and Tebaldi, 2004; Viceto et al., 2019) within boreal forest soils may greatly alter soil food web dynamics and potentially ecosystem-level properties.

Members of the genera *Asca* (family: Ascidae) and *Veigaia* (family: Veigaiidae) are often found together within forest habitats (Hurlbutt, 1968). These genera are considered generalist predators as individuals have consumed both arthropod and nematode prey in feeding experiments (Walter, 1988), but differ in size as *Veigaia* species tend to be larger (500 – 1000+ µm in body length) than *Asca* species (300 – 400 µm) (Hurlbutt, 1984, 1963). Interestingly, these genera contain a disproportionate number of parthenogenetic species (i.e., thelytokous parthenogenesis (all-female species); Norton et al., 1993) compared to the rest of Mesostigmata. *Asca garmani* is presumed to be parthenogenetic as observable males are absent within their populations (Walter and Lindquist, 1995). *Veigaia mitis* appears to vary between sexual and parthenogenesis reproduction modes, as populations in southern United States (Maryland and North Carolina) have both males and females (Hurlbutt, 1984), while populations of *V. mitis* in northern United States (New Hampshire, Connecticut, and Massachusetts) and Canada are parthenogenetic. Indeed, I did not observe any male individuals for either of these species in my study. Given the increase in the abundance of these two species, particularly *V. mitis* as their abundances were nearly 9×, under warming in this

experiment, it suggests that parthenogenetic species may benefit from warming through increased reproductive output. These results align with Lindo (2015), who found that warming increased the abundance of parthenogenetic species, particularly within the families Brachycthoniidae and Suctobelbidae, in oribatid mite communities. Less than 1% of all animals are thelytokous parthenogens (Norton and Palmer, 1991), but for mites, particularly oribatid mites, thelytokous parthenogenesis is common (Norton et al., 1993). About 9% of Oribatida species are parthenogenetic, as entire families contain no known sexual species (e.g., Malaconothridae, and Tectocephidae). Thelytokous parthenogenesis is also relatively well studied within Oribatida, compared to Mesostigmata. Past studies have found parthenogenetic oribatid species and their populations recovered faster to environmental change (i.e., drought) than sexual species (Lindberg and Bengtsson, 2005). This could be because parthenogenetic species have a reproductive advantage over sexual species as parthenogenetic species have no mating costs and can start a population with a single individual (Schneider et al., 2007). Parthenogenetic species also have a higher effective reproductive rate than sexual species as every viable offspring can reproduce (Norton, 1994). Potentially, a reproductive advantage for parthenogenetic species like *A. garmani*, but mainly *V. mitis*, may explain their increased abundances at 20 °C.

Gamasellus vibrissatus Emberson, which I also observed in my study, also reproduces via thelytokous parthenogenesis, as no males are known (Emberson, 1967; Norton et al., 1993) but was unaffected by warming. Meaning not all parthenogenetic species in this study benefited from increasing temperatures. Differing responses to warming between parthenogenetic species may come down to feeding preferences and the nutritional quality of prey, as diet can impact reproductive output for mesostigmatic mites (Walter et al., 1987), including those that are parthenogenetic (Moreira et al., 2015). Walter et al. (1987) found that generalist feeding mesostigmatic species reared on nematodes had lower larva to adult development times than when reared on arthropods. Additionally, Walter et al. (1987) found that some mesostigmatic mite species only produced eggs when feeding on nematodes. This suggests that arthropods are less 'nutritious' than nematodes. Feeding experiments have shown that *Gamasellus*, like *Asca* and *Veigaia*, will feed on both arthropods and nematodes, making them generalist

feeders (Beaulieu and Walter, 2007). But at the species-level, mouthpart (cheliceral) morphology can affect feeding preferences for mesostigmatic mites (Bowman, 2021; Buryn and Brandl, 1992; Walter and Ikonen, 1989). Chelicera are claw-like appendages that are used by mesostigmatic mites for food acquisition (Krantz, 2009a) and for soil arthropods, cheliceral morphology can dictate feeding preferences (Kaneko, 1988; Perdomo et al., 2012). An extensive review by Bowman (2021) found that cheliceral morphology may dictate Mesostigmata feeding preferences as the length of the entire chelicerae, the length and shape of chelicera digits, and the ‘crunch force’ (i.e., the estimated force between the tips of the chelicera digits) affects prey selection by individuals. I observed that the chelicerae of *A. garmani*, *V. mitis*, and *G. vibrissatus* differ from one another, with respect to the size of their cheliceral digits, and the number and ornamentation of teeth on each digit. Suggesting, possible differences in feeding preferences among these three species may explain the differences in their abundance under warming. For instance, a nematode-rich diet for both *A. garmani* and *V. mitis* may have facilitated their increased reproductive output under warming, leading to higher abundances at 20 °C, while a diet consisting primarily of arthropods for *G. vibrissatus* may have limited their reproductive output. Although it is not fully clear why parthenogenetic species showed taxon-specific responses to warming, my study highlights the utility of knowing a species traits, as a trait-based approach may better explain changes to soil communities to climate warming than community indices alone (Bokhorst et al., 2012).

I found that some sexual species (based on the presence of both female and male individuals found within my mesocosms) also had higher abundances under warming. Species such as *Z. nr. carolinensis* and *Dinychus* sp.1 were more abundant at 20 °C, compared to 12 °C. But, for both these species, individuals were highly concentrated within 2 – 3 mesocosms (out of 12 mesocosms at 20 °C), meaning their abundances were highly variable. As ectotherms, warming promotes Mesostigmata reproduction as population growth rate increases and generation time decreases at higher temperatures (Lee and Gillespie, 2011; Wang et al., 2014). Although both sexual and parthenogenetic species would benefit from rising temperatures, in my study, it appears changes to assemblage composition were mostly driven by increases in parthenogenetic species,

particularly *V. mitis*, as their average abundances were more than eight times greater at 20 °C.

Mites, collembolans and nematodes showed group-specific responses to warming. Specifically, I found that the overall abundances of oribatid mites, collembolans, and nematodes were unaffected by warming in my study. However, I found that astigmatic mite abundance greatly increased at 20 °C, compared to 12 °C. Astigmatic mites have invaded numerous habitat types, such as soil, animal dung, caves, stored food products, and are known animal associates (OConnor, 2009). Soil astigmatic mites thrive in patchy habitats that are rich in organic matter (Coleman et al., 2018; OConnor, 2009). Astigmatic mites also have high fecundity, along with fast development and turnover rates, making them *r*-selected (Norton, 1994). Although long-term warming (20 years) has shown not to impact the overall abundances of astigmatic mites (Alatalo et al., 2017), similar to my study, short-term warming (18 months) has shown to be beneficial (Lindo, 2015). Conversely, warming led to fewer prostigmatic individuals compared to ambient conditions at 12 °C. Prostigmata occupy numerous niches and trophic levels within soil food webs, as individuals can be fungivores, predators, and consume microflora (Krantz, 2009b). Past studies have also found prostigmatic mites are susceptible to higher temperatures with lower overall abundance observed at higher temperatures (Briones et al., 2009; Wu et al., 2014), suggesting warming is detrimental, either directly through increased metabolic demands (Gillooly et al., 2001), leading to greater starvation risks (Rall et al., 2010; Vucic-Pestic et al., 2011), or indirectly through top-down control by mesostigmatic mites (Usher et al., 1989). Although many prostigmatic mites are predators, most species are soft-bodied and are a potential food resource for mesostigmatic mites. As warming can increase feeding rates for mesostigmatic mites, (Jensen et al., 2017; Ramachandran et al., 2021), increased intraguild predation by mesostigmatic mites may have lowered their abundances. My results highlight that short-term intensive warming does not affect the overall abundances of higher taxon groups similarly, meaning alterations to food web topology and dynamics should be expected under climate change.

4.4.1 Implications of changing Mesostigmata assemblages for the soil food web

The increased abundance of larger-bodied predators, mainly *V. mitis*, could greatly impact soil communities and food web dynamics. This is, in part, because larger mesostigmatic individuals may increase top-down control onto prey as larger-bodied individuals have higher feeding rates than smaller-bodied ones (Walter and Ikonen, 1989). In addition, although the abundance of Zerconidae, which have been shown to feed exclusively on nematodes (Walter, 1988) remained high at 20 °C, the increased presence of generalist predators like *A. garmani* and *V. mitis* may alter soil food web dynamics through the changing proportion of generalist and specialist predators within Mesostigmata assemblages. First, intraguild predation should increase (Polis et al., 1989) as generalist feeding mesostigmatic individuals may consume soft-bodied predators, like some prostigmatic mites (Usher et al., 1989), juvenile mesostigmatic mites (Peschel et al., 2006) and/or smaller, nematode-feeding predators (Laakso and Setälä, 1999). Increased predation on nematode-feeding mesostigmatic mites may decrease top-down control on nematodes because specialist predators have greater top-down control on their prey populations than generalists (Laakso and Setälä, 1999). Conversely, the increased abundance of generalist predators may strengthen feeding on arthropod prey, like soft-bodied mites and collembolans (Schneider and Maraun, 2009). In general though, top-down control may strengthen in soil food webs because of the increased feeding rate of mesostigmatic mites at higher temperatures (Jensen et al., 2017; Ramachandran et al., 2021). Increased feeding rates under warming may induce top-down cascades towards microbial communities and impact ecosystem-level properties, such as detritus decomposition (Lang et al., 2014), further altering soil food web dynamics.

4.4.2 Conclusions

Mesostigmatic mites are essential contributors in the soil food web due to their high trophic position and by regulating prey abundances through top-down control (Hunt et al., 1987; Moore et al., 2003; Schneider and Maraun, 2009). Therefore, knowing how increasing temperatures shifts Mesostigmata assemblages is important to understanding soil food web dynamics in a warmer world. Short-term, intensive warming will greatly

impact boreal forest soils as my study showed that warming shifts the assemblage composition of the most abundant predators within boreal forest soils, mesostigmatic mites. Specifically, warming benefited parthenogenetic species, particularly *V. mitis*, as previously observed with oribatid mites (Lindo, 2015). Although long-term warming may affect Mesostigmata assemblages differently, my study showed that reproductive mode plays a critical role in shaping soil predator communities under short-term warming. This study provides further insight on the effect of warming on Mesostigmata at the community-level, as well as showing that short-term, intensive warming will impact multiple soil fauna groups.

4.5 References

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Chapter 5

5 Discussion

5.1 Summary of findings

Ectothermic predators are living under a rapidly changing climate. Because ectothermic predator metabolic and physiological rates are tied to environmental temperatures, climate change impacts individual-level functions and processes (Clarke, 2017), but the effects of which may accumulate at higher ecological levels (i.e., populations, communities, and ecosystems). To better isolate the effects of climate change on ectothermic predators, I examined predator feeding behaviour, predator-prey dynamics and predator communities across three ecological levels (individual-, population-, and community-level) using mesostigmatic mites as my model predator. I found that predators fed more on small-bodied prey, but not the large-bodied prey, which consequently lowered their estimated energy intake (individual-level; Chapter 2). At the population-level, predator populations were relatively invariant across temperature and variability treatments as their inclusion within mesocosms consistently lowered prey abundances. But average prey body size increased under warming as predators shifted prey body size distribution (population-level; Chapter 3). Finally, predator communities shifted under short-term intensive warming, primarily due to an increased abundance of a single parthenogenetic species, *Veigaia mitis* (Berlese) (community-level; Chapter 4).

5.2 General discussion

Several consistent themes emerged from my research. First, predator and/or prey body size factored into all three experiments as predators either altered prey body size distributions (Chapter 3), predator community body size distributions shifted with species composition under warming (Chapter 4), or prey body size affected predator feeding rate and behaviour under warming (Chapter 2). The importance of body size emerging across the individual-, population- and community-level illustrates the importance of individual body size in predator-prey interactions, but as well, that changes in ecosystem function

and processes under climate change may possibly be traced back to shifting body size distribution within communities (for further commentary, see section 5.3). Second, underscoring my results were that predator reproduction and feeding mode (Chapters 3 and 4), predator nutrient demands and intake (Chapters 2 and 4), and predator and prey temperature preferences and limits (Chapter 3), impacted predator-prey interactions and predator community composition.

The reproductive mode of individuals played a surprising role in shaping predator response to warming. *Veigaia mitis* and *Asca garmani* – species that had higher abundances with warming in Chapter 4 – are both parthenogenetic. Past studies have shown parthenogenetic oribatid mite species increased in abundance at higher temperatures (Barreto et al., 2021; Lindo, 2015), suggesting that parthenogenetic reproduction is one attribute that may be favoured under climate change, at least in these two groups. But parthenogenesis alone does not fully explain my experimental results. Both *S. scimitus* (model predator species in Chapter 3) and *Gamasellus vibrissatus* (another parthenogenetic predator species from Chapter 4) abundances remained low after prolonged exposure to warming.

To thrive in warmer environments, ectothermic predators will need to shift the timing of seasonal and daily activities, events, and behaviours to maximize performance and match prey availability (Damien and Tougeron, 2019; Durant et al., 2019; Powers et al., 2018). But the underlining prey quality and the nutrient demands of predators will also contribute to their changing population abundances under warming. For instance, mesostigmatic mites develop faster when reared on higher-quality nematodes, compared to lower-quality arthropods (Walter et al., 1987). Therefore, a diet rich in nematodes may explain why some predators, like *V. mitis*, and not others increased in abundance under warming. But importantly, arthropod prey themselves differ in nutritional quality. In Chapter 2, I found that *F. candida* and *O. nitens* were more energy dense than *C. lactis*, and presumably, mesostigmatic mite prolonged consumption of lower-quality arthropod prey will contribute to poor performance (growth and development) under climate change. Similar to an ecological trap (i.e., where an individual makes a maladaptive choice under changing environmental conditions; Schlaepfer et al., 2002), mesostigmatic species populations may decline if changing feeding behaviour leads to increased

consumption of lower quality prey. This was observed in Chapter 2 as predators fed more on small-bodied, energy-poor prey at 24 °C, which lowered their estimated energy intake under warming. In general, as metabolic demands continue to rise for ectothermic predators, access to high quality, energy-rich prey may improve their survival under climate change, but predators then need to consume such prey to reap its benefits.

Stratiolaelaps scimitus, like many other mesostigmatic mites, is an active predator as individuals continually move, searching for their prey. Movement expends energy that would otherwise be conserved in sit-and-wait predator species. In snakes, active predators also have greater maintenance costs than sit-and-wait predators (Dupoué et al., 2017). It is unknown/unclear whether this trend is ubiquitous across other ectothermic predator groups but may suggest that active predators will be impacted more by rising metabolic demands from climate change than sit-and-wait predators, due to higher maintenance costs and additional energy expenditure from movement. This could explain why predator populations did not increase at higher temperatures in Chapter 3; high metabolic demands limited the energy available for reproduction. Whether sit-and-wait predators will outcompete active predators under climate change, remains unknown; however, Barton and Schmitz (2009) found that warming increased encounters between an active and sit-and-wait spider species in a grassland system, leading to extinction of the active spider species due to intraguild predation. While it appears that active predators will be particularly sensitive to higher temperatures with climate change, further examination is needed to dissect how predator feeding mode dictates their success under climate change.

Considering the temperature-performance relationship is critical to predicting species response to warming and predator-prey outcomes. Smaller populations of the prey *F. candida* occurred with increased exposure to 26 °C in Chapter 3 in the absence of predators, which suggests this temperature exceeds their T_{opt} (Mallard et al., 2020; Snider and Butcher, 1973), while no change in population size was observed for *S. scimitus*. These findings and conclusions have important implications for integrated pest management (IPM), where a single predator species is used to reduce pest populations, and a mismatch between predator and prey T_{opt} and CT_{max} might alter the efficacy of IPM strategies. For instance, if T_{opt} and CT_{max} is higher for the pest prey than their predator, a

prolonged exposure to extreme warming might reduce top-down control. Coombs and Bale (2013) reported that the biocontrol predator mite *Phytoseiulus persimilis* upper lethal limit (i.e., when a heat coma is induced) is 7 °C lower than their prey, the pest species *Tetranychus urticae* (the two-spotted spider mite). This suggests the utility of *P. persimilis* as a biocontrol predator may be limited under climate change if prolonged heat waves decimate populations. The status of biocontrol predators should be re-evaluated if thermal preferences and physiological limits are lower than their target species, and such information should be incorporated into management decisions.

5.3 Future research: Scaling to ecosystems using a trait-based approach

Establishing general trends in ecology is challenging, particularly at the community-level, due to the interactions of tens, hundreds, or even thousands of species (Lawton, 1999). But understanding how communities respond to climate change is critical to predicting changes to ecosystem-level functions and processes that will impact management and conservation decisions. In my research, measuring individual-level characteristics of species (e.g., body mass) and having detailed species-level information of morphology and physiology were crucial in the interpretations of my community-level results. Knowing the natural history, physiology, and ecology of species that comprise communities is vital to understanding how climate change will shape ecological communities, which can be performed by implementing a trait-based approach.

Traits are morphological, physiological, behavioural or other features measured at the individual-level (Violle et al., 2007) and can be categorized by their response to environmental change (response trait) and their effect on ecosystem function (effect trait) (response-effect trait framework, *sensu* Lavorel and Garnier, 2002). Response traits are filtered out of communities due to both abiotic and biotic constraints (Webb et al., 2010), like with climate change, shifting the trait distribution within the final community, with the leftover effect traits then dictating ecosystem function. Ideally, the best traits to examine are ones that respond to environmental change and effect ecosystem function (Suding et al., 2008). For example, Larsen et al. (2005) found that dung beetle and bee

body mass was both a response and effect trait, as larger beetles and bees were more extinction prone (response trait), while larger individuals had greater dung burial and pollination efficiencies (effect trait). In general, the accumulation of species interactions govern ecosystem-level functions, but the interactions themselves are mediated by species traits. Therefore, quantifying trait distribution within communities can help predict how climate change impacts ecosystem function as it is species traits that drive these interactions.

In my research body size appeared as an important trait throughout my experiments. Body size responded both directly (through changing growth rates) and indirectly (through predator feeding behaviour and rate, reproduction mode of a subset of species) to warming at the individual-, population-, and community-level and was crucial in my interpretations of how climate change may affect ectothermic predator feeding behaviour, predator-prey dynamics, and hypothesizing how shifting predator communities will impact soil food webs. In general, individual body size is correlated with metabolic rate, population size, trophic position, and disturbance sensitivity for species (Brose et al., 2006; Brown et al., 2004; Cardillo, 2003; Woodward et al., 2005), making body size a universal trait (i.e., a singular trait that explains others). Community body size distributions have been shown to affect several ecosystem-level processes, like decomposition (Dossena et al., 2012), energetic fluxes within food webs (Ledger et al., 2013; Potapov et al., 2019), ecosystem respiration and gross primary production (Yvon-Durocher and Allen, 2012), and carbon and nutrient cycling (Hébert et al., 2017). For an example with predators specifically, in Barley fields, a greater community weight mean of body size (CWM) amongst predators (e.g., spiders and beetles) was correlated with lowered predation rates on aphids, a notorious pest species (Rusch et al., 2015). It was hypothesized that greater CWM for predators corresponded with increased intraguild predation by larger beetles on smaller spiders, which freed aphids from predation. Calculating the CWM of body mass (or size) for communities, predator and prey communities separately, and even predator-prey mass ratio within communities may offer potential insight on the effect of climate change on predators and ecosystems. My experiments in Chapters 3 and 4 provide examples of how body size measurements can be incorporated within future studies, but analyzing how these metrics shift ecosystem

functions, like ecosystem respiration and gross primary production, remains the next steps to be taken.

Attempting to fully resolve how climate change affects ectothermic predators is immensely challenging. Processes (or traits) that drive individual behaviour and dynamics become more obscure at higher ecological levels, as emergent properties arise due to community interactions, such as predation, competition and mutualism, that are not observable at the individual-level. Instead, one can isolate how climate change affects ectothermic predators and establish if the same pattern emerges across multiple ecological levels. I found that body size was essential in explaining predator-prey interactions and predator communities, establishing that body size a key determinant in understanding how climate change will affect ectothermic predators. Understanding how body size distributions respond to climate change and the subsequent effect of ecosystem function should be the focus of future research on ectothermic predators.

5.4 Caveats and limitations of study design

Results from scientific experiments should always be contextualized by the methodology conducted, and my doctoral research is no different. In ecology, manipulative field experiments are the gold standard as it allows researchers to test hypotheses in a field setting. My doctoral research relied exclusively on feeding and mesocosm experiments, instead of field manipulative studies. Controlled laboratory settings limit confounding factors but fundamentally reduce realism (De Boeck et al., 2015) as multiple environmental parameters usually respond to a single treatment. For example, warming on belowground environments typically reduces soil moisture content (Holmstrup et al., 2017; Vestergård et al., 2015) which may, in part, dictate soil animal community response to simulated warming. In Chapter 4 I maintained the gravimetric moisture content within the mesocosms to better detect the direct responses of soil mesostigmatic mites and their prey groups to intensive warming but recognize warming-induced changes to other abiotic environmental conditions may alter these experimental outcomes in natural settings. Furthermore, by examining predator-prey dynamics within a simplified setting (such as in Chapter 2), it may lead to over-estimating or -interpreting

treatment effects. For instance, the attack rates of the benthic isopod *Saduria entomon* on the amphipod *Monoporeia affinis* were 400× greater in a feeding experiment versus what was observed in the field (Aljetlawi et al., 2004). However, similar and consistent results on the effect of predators on prey body size were seen in both Chapters 2 and 3, where the Chapter 2 experiment was performed in a feeding arena, while Chapter 3 had increased habitat complexity (a 3-D heterogeneous environment from the vermiculite), suggesting increased habitat complexity did not impact predator feeding in my experiments.

A major concession when conducting my experiments was that I did not reproduce daily temperature cycles that ectothermic predators (and their prey) reside in, due to infrastructure and apparatus limitations. Past studies have used outdoor mesocosms (for aquatic systems) (e.g., Dossena et al., 2012; Kratina et al., 2012; Shurin et al., 2012; Yvon-Durocher et al., 2015, 2011), open top chambers (for soil systems, with passive and/or active warming) (e.g., Alatalo et al., 2017; Barreto et al., 2021; Kardol et al., 2011; Markkula et al., 2019; Meehan et al., 2020), or a natural warming gradient, like geothermal hotspots (e.g., Holmstrup et al., 2018; Sohlström et al., 2021) to better replicate natural conditions. For in-lab mesocosms, programming incubators with day-night temperature cycles can more closely mimic natural diurnal conditions (e.g., Thakur et al., 2018, 2017), yet my experimental temperatures were constant in Chapter 2 and 4, and throughout the day in Chapter 3. Instead of metabolic and physiological rates for predators and prey rising and falling with diurnal temperatures, rates would remain constant throughout the duration of the experiment. In Chapter 3, the constant exposure to optimal temperatures for *F. candida* led to the largest population size in both the cool and warm temperature range. So, within the context of my research, constant exposure, specifically to optimal temperatures, probably leads to higher performance than otherwise would be expected under a natural temperature cycle.

What is also unclear is whether the timing of Chapter 4 experiment affected the outcome, specifically through altered phenological population events. Given that the mesocosm substrate and associated communities were collected and the experiment started in October, natural seasonal progression (i.e., winter) did not occur in my in-lab experiment as I maintained mesocosms at either 12 °C or 20 °C. Although these

temperatures are similar to average (or predicted) growing season temperatures, both these temperatures are higher than field conditions between October and January where air temperatures normally drop below 0 °C (Webster and McLaughlin, 2010). Although snow can insulate belowground communities from extreme coldness (Convey et al., 2015), soil fauna will still experience sub-zero temperatures. As temperatures exhibited in Chapter 4 do not reflect the natural conditions, I suspect that warming triggered higher growth and reproduction rates than during the usual cold winter months. But importantly, resource availability likely dictated their persistence under these warmer than normal winter temperatures. Anderson, (1975) found that resource availability and diet strongly factored into oribatid mite species persistence in both the summer and winter months in Chestnut and Beech litter. So, although temperatures were higher than normal, similar mechanisms (i.e., diet and consumption) still likely dictated mesostigmatic mite and arthropod and nematode prey persistence during my experiment. For predator mite species like *V. mitis*, this possibly came from feeding on nematodes, which led to their increased abundances at 20 °C. At the very least, cold tolerance strategies by soil fauna were not invoked during my experiment which would be expected under natural conditions for that time of year (Anthony et al., 2016; Anthony and Sinclair, 2019; Holmstrup et al., 2002; Sørensen and Holmstrup, 2011).

Finally, my research relied on a single predator group, mesostigmatic mites, which may limit some interpretations when extending my results to other ectothermic predator groups. For instance, mesostigmatic mites are dissimilar to many predators because they can consume prey both smaller and larger than themselves (Bowman, 1987; Cabrera et al., 2005; Rahmani et al., 2016; Usher and Bowring, 1984; Xie et al., 2018), and are fluid-feeders who extra-orally digest (EOD) their food before consumption (Cohen, 1995). As a result, prey body size is not as limiting for mesostigmatic mites as for other predators like fish, where gape (mouth) size dictates food intake. Another unique feature as stated earlier, is the high propensity for mesostigmatic mites to be parthenogenetic, which is typically rare in the natural world (Norton et al., 1993), meaning the community shifts observed in Chapter 4 would not arise because of that specific mechanism in most other systems. That said, in general, mesostigmatic mites are excellent model predators because they are small, highly abundance and diverse, are

generalist feeders, and can be easily sampled and reared, but feeding and reproduction modes distinguish mesostigmatic mites from other ectothermic predators.

5.5 Conclusions

In my doctoral research I investigated the effect of climate change across multiple ecological levels (individual-, population-, and community-level) to isolate how warming affects ectothermic predators, using mesostigmatic mites as my model organism. I found 1) that predators increased their feeding on small-bodied prey, which lowered their estimated energy intake (individual-level; Chapter 2). 2) Prey population sizes were affected greatly by temperature, but the effects of predation remained constant, as predators greatly lowered prey abundances and increased prey body size (population-level; Chapter 3). And 3) predator communities shifted under warming at 20 °C, which was primarily due to the increase of a single parthenogenetic species, *Veigaiia mitis* (community-level; Chapter 4). Together, I found that body size factored into predator-prey dynamics at all three ecological levels. Going forward, I propose that body size should be considered when examining thermal-mediated predator-prey dynamics. This can be achieved using a response-effect trait framework where community-level body sizes and predator-prey mass ratios are evaluated against ecosystem-level functions. Disentangling how climate change affects ectothermic predators is challenging, due to species- and function-specific responses to temperature change paired with species interactions across various temporal and spatial scales. Instead focusing on how climate change is driving ecosystem functions through changing predator communities and predator-prey dynamics will be critical in our understanding of what lies ahead for ecological communities.

5.6 References

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Appendices

Appendix A Chapter 2 Supplementary Material

Energy demands of Stratiolaelaps scimitus individuals

Energy demands ($\text{mJ} \cdot 8 \text{ h}^{-1} \cdot \text{individual}^{-1}$) of an individual *S. scimitus* were calculated at 16 °C for 16 °C-maintained individuals and 24 °C for 24 °C-maintained individuals using measured CO_2 production (Williams et al., 2015). I converted CO_2 production into metabolic rate using two equations, first converting $\dot{V}\text{CO}_2$ (i.e., measured CO_2 production rate) to $\dot{V}\text{O}_2$, assuming a respiratory quotient (RQ) of 0.8 (Lighton, 2008):

$$VO_2 = VCO_2 / RQ \quad (1)$$

I then converted $\dot{V}\text{O}_2$ into metabolic rate in Watts (J sec^{-1}) using the oxyjoule equivalent:

$$\text{oxyjoule equivalent} = 16 + (5.164 * RQ) \quad (2)$$

$$\text{Metabolic rate} = VO_2 * \text{oxyjoule equivalent} \quad (3)$$

Next, assuming that energy demands are equal to the average individual metabolic rate, I divided the measured metabolic rate by the number of predators measured (i.e., 25 individuals), multiplied by the number of seconds in eight hours, and converted into millijoules (multiplied by 10^3):

$$\text{Individual Energy Demands} = (\text{Metabolic Rate} / 25) * 28800 * 10^3 \quad (4)$$

Calculating energy demands for individual predators allowed me to compare energy lost through respiration relative to the energy intake during the feeding trials.

Calculating body mass and energy content for predators and prey

For each species, I estimated the total energy content (mJ individual⁻¹) from the average mass of each metabolic substrate (lipid, protein), the proportional body composition of each metabolic substrate, and body mass. I used two formulas to calculate the body mass for each taxon, one for mite species (*C. lactis*, *O. nitens*, and *S. scimitus*), and another for *F. candida*. For mites, I used the formula derived from Caruso & Migliorini (2009):

$$\mu g = \left(\frac{4\pi}{3}\right) * \left(\frac{0.201 * ((L + W)^3)}{1,000,000}\right) \quad (5)$$

where L = length in μm of a mite, and W = width in μm .

For *F. candida*, I used the formula derived from Edwards, (1967)

$$\mu g = (3.06 * L)^3 \quad (6)$$

where L = length of *F. candida* in mm.

I derived length and width for each taxon from available literature and species descriptions. For *S. scimitus*, I used the average length and width of adult females from a re-description of the species in Walter and Campbell (2003), where length was 640 μm , and width 400 μm . For *O. nitens*, I used lengths and widths found in Fajana et al. (2019), where length was 510 μm and width was 290 μm . For *C. lactis*, I averaged out the reported lengths of adults and juveniles (but not larva), which came to an average of ~300 μm (Zhan et al., 2017). The width of *C. lactis* was not recorded in available literature. As they are oval in shape, I assumed that length was 1.67 \times greater than width, meaning I used a width of 180 μm to calculate the body mass of a single *C. lactis*. Body length of *F. candida* ranged from 700 μm – 2000 μm in our choice and no choice feeding trials. Because of this, I choose an approximate average body length of 1000 μm to calculate the body mass of a single *F. candida*.

For each taxon i (*S. scimitus*, *F. candida*, *C. lactis*, *O. nitens*) I calculated their total energy content EC (mJ individual⁻¹) at each temperature T (16 °C or 24 °C) – to subsequently determine predator energy intake during the choice feeding trials –

assuming a constant energy density of soluble proteins (17.8 J mg⁻¹) and neutral lipids (39.3 J mg⁻¹) (Schmidt-Nielsen, 1990). Total energy content was thus calculated as:

$$EC_{i,T} = \sum_i^t (M_T \times ED_k) \times W_i \quad (7)$$

where EC is the total energy of a single individual of species i (mJ individual⁻¹) at temperature T (16 °C or 24 °C), M_T is the proportional concentration of each macromolecule type at temperature t (16 °C or 24 °C), ED is the energy density for a given macromolecule k (protein or lipids), and W_i is the body mass (mg) of each species.

Estimated energy intake of Stratiolaelaps scimitus during the choice feeding experiment

I estimated energy intake during the choice feeding trials using predator feeding rate and prey energy density that were derived from measurements in this experiment, and changes in predator body mass from two separate experiments examining *S. scimitus* feeding at 16 °C and 24 °C on either *C. lactis* or *F. candida*. In both experiments, *S. scimitus* was purchased from Koppert Canada Limited and maintained at 20 °C on a diet of adult and juvenile *F. candida*. Change in predator body mass was calculated based on feeding trials of a single *S. scimitus* individual in an arena (40 mm diameter with plaster of Paris substrate) with ten *F. candida* or ten *C. lactis*. All predators were food deprived for 24 h prior to feeding trials, and feeding trials lasted four (*F. candida*) or two hours (*C. lactis*). I calculated the body mass of *S. scimitus* before and after the feeding trial using morphometric body size measurements of each individual converted to body mass using length-mass formulas. Predator body size measurements were made on immobilized predators positioned dorso-ventrally (see Ramachandran et al. (2021) for more details) to determine the change in body mass ($\mu\text{g prey eaten}^{-1}$) using the formula:

$$\text{Change in predator body mass} = \frac{\text{Body mass after feeding} - \text{body mass before feeding}}{\text{number of prey eaten}}$$

Values for these parameters are presented in Table 1A on the next page

Table 1A *Stratiolaelaps scimitus* change in body mass (μg prey eaten⁻¹) when feeding on *C. lactis* and *F. candida* at 16 °C and 24 °C. Values for *C. lactis* were derived from experimental measurements in Ramachandran et al. (2021), while values for *F. candida* were taken from unpublished data. Note, that *S. scimitus* feeding at 24 °C versus 16 °C equates to a lower change in body mass for both prey species.

Taxa	Temperature (°C)	Change in body mass (μg prey eaten ⁻¹)
<i>C. lactis</i>	16	2.3
	24	1.3
<i>F. candida</i>	16	6.0
	24	5.7

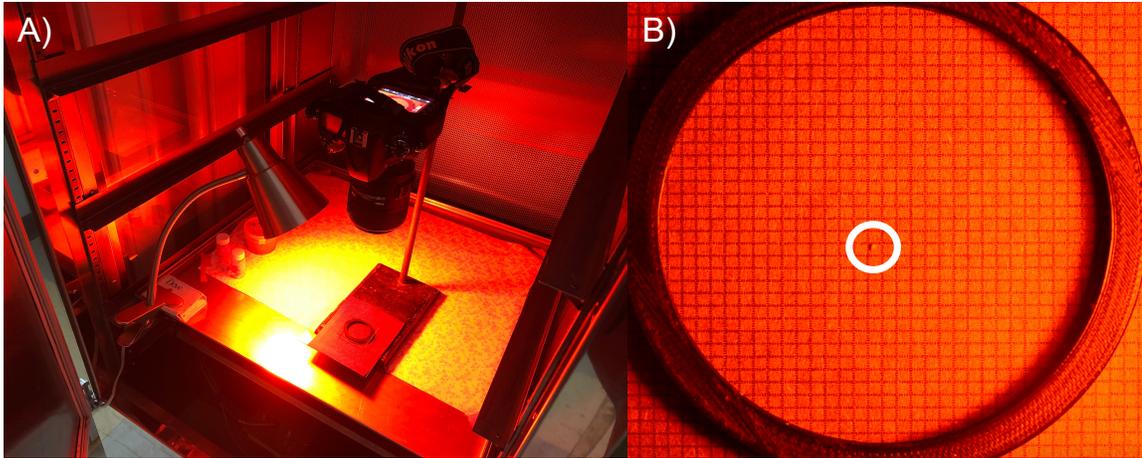
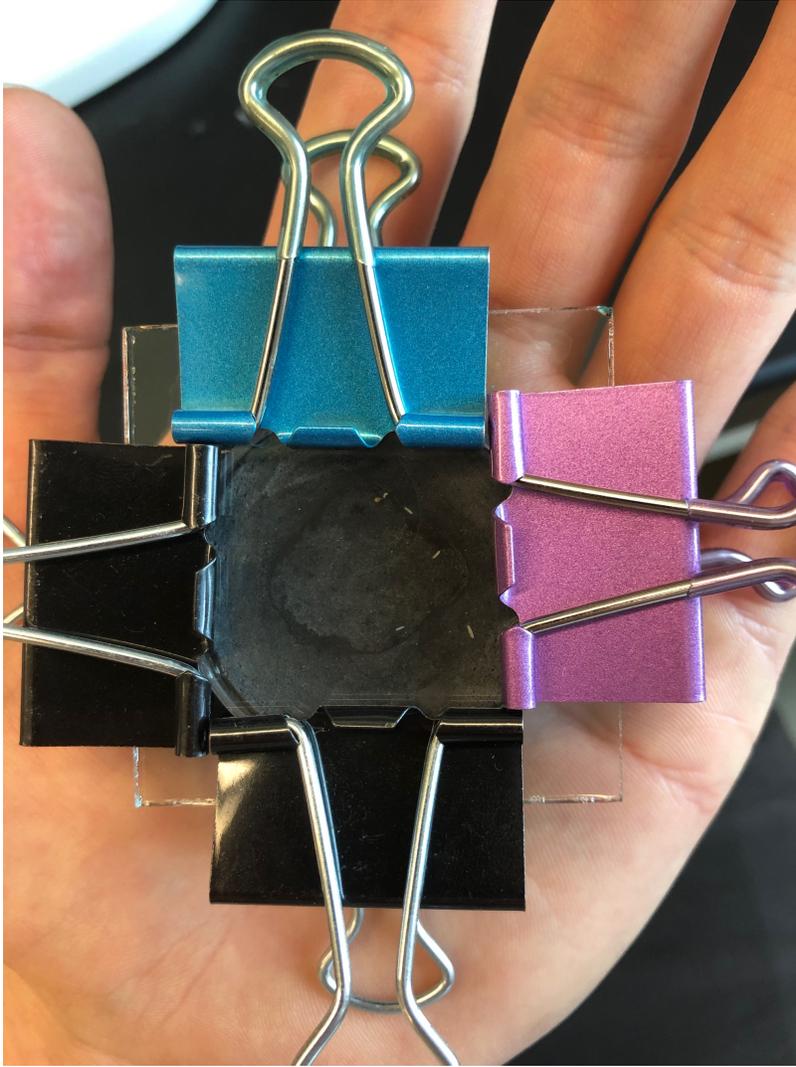


Image 1A A) A photograph showing the set up for movement trials. A closed GCHA-10 Environmental Growth Chamber housed the movement arenas, which were illuminated during trials with a red LED light. B) A still image of a movement trial recording for *S. scimitus* (individual is in the center of the grid in the white circle).



1

2 **Image 2A** A photograph of the arenas used in the choice and no choice feeding trials. The
3 feeding arena consisted of a 40 mm petri dish containing of 9:1 ratio of plaster of Paris and
4 activated charcoal. I observed feeding through a small, 5 × 5 cm glass covering held on top
5 of the petri dish by four 32 mm binder clips. This photograph shows an on-going, no
6 choice feeding trial of *F. candida* at 16 °C.

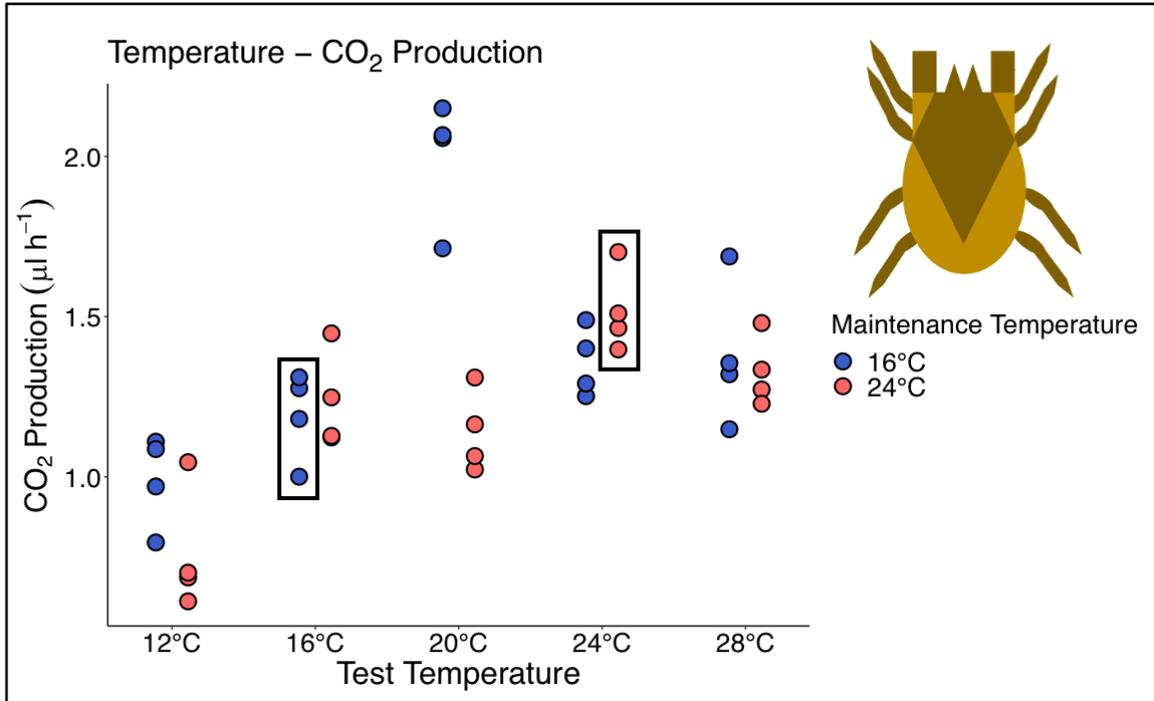


Figure 1A Temperature – CO₂ production relationship for *S. scimitus* maintained at 16 °C and 24 °C. Test temperatures that were measured were 12 °C, 16 °C, 20 °C, 24 °C, and 28 °C. Boxes indicate experimental conditions that were used in feeding trials, as well as to measure total lipid and protein content, and movement rate. These values were analyzed with a one-way ANOVA to test for significant differences in metabolic demands for predators at 16 °C and 24 °C ($F_{1,6} = 11.69$, $P = 0.014$). Information on methods used to measure CO₂ production is in *Stop-flow Respirometry of S. scimitus* within the main text.

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Appendix B Chapter 3 Supplementary Material

Estimates of metabolic rate and consumption of S. scimitus during the experiment

I estimated the metabolic (J 40 days⁻¹ individual⁻¹) and consumption rate (number of *F. candida* eaten 40 days⁻¹) of *S. scimitus* during the experiment for each temperature treatment. To do this, I used experimental values derived from Chapter 2. First, I converted *S. scimitus* CO₂ production (μl h⁻¹) into metabolic rate using methods described in Appendix A (section: *Energy Demands of S. scimitus Individuals*). I excluded CO₂ production values where test temperatures appeared to be higher than T_{opt} for *S. scimitus* (for 16 °C maintenance temperature, 24 °C and 28 °C test temperatures; for 24 °C maintenance temperature, 28 °C test temperature). Thereafter, I plotted values and attained the Line of Best Fit (Figure 1B). Using the equation from Line of Best Fit, I estimated the metabolic demands of *S. scimitus* at 12 °C constant, 20 °C constant, and 26 °C constant (Table 1B). For *S. scimitus* individuals that were exposed to more than one temperature, I used a community weighted mean to calculate their metabolic demands:

$$\text{CWM metabolic demands} = \sum (p_T \times MR_T),$$

Where p_T is the proportion of time spent at Temperature T (12 °C or 20 °C / 20 °C or 26 °C) and MR is the estimated metabolic demands at Temperature T (Table 1B).

I estimated the consumption rate of a *S. scimitus* individual by dividing the metabolic demands of *S. scimitus* with the energy intake of predators when feeding on a single *F. candida*. I calculated energy intake by multiplying the macromolecule concentration and energy density of soluble protein and neutral lipids with the change in *S. scimitus* mass when feeding on *F. candida* using the following equation:

$$EI = \sum (M_k \times ED_k \times W)$$

where EI = is the total energy of a single individual of species ($J F. candida \text{ eaten}^{-1}$), M is the average concentration of macromolecule k (proteins (0.191) and lipids (0.124)), ED is the energy density for a given macromolecule k (protein ($17.8 J \text{ mg}^{-1}$) or lipids ($39.3 J \text{ mg}^{-1}$)), and W is the change in mass ($0.00585 \text{ mg } F. candida \text{ eaten}^{-1}$).

Finally, to calculate the consumption rate of *S. scimitus* during the experiment I used the following equation:

$$CR_{Tt} = \frac{MR_{Tt}}{(EI * A_e)}$$

Where CR_{Tt} is the consumption rate of an *S. scimitus* individual (number of *F. candida* eaten 40 days^{-1}) at temperature treatment Tt , MR is the estimated metabolic rate over 40 days at temperature treatment Tt , EI is the energy intake of *S. scimitus* when feeding on *F. candida* ($0.048 J F. candida \text{ eaten}^{-1}$), and A_e is the assimilation efficiency of predators (0.85; Jochum et al., 2017).

Values for metabolic and consumption rate are presented in Table 1B.

Table 1B Estimated metabolic and consumption rates for a *S. scimitus* individual for each temperature treatment during the experiment.

Temperature Treatment	Ratio of time spent at each temperature	Estimated Metabolic Rate (J 40 days ⁻¹ individual ⁻¹)	Estimated Consumption Rate (number of <i>F. candida</i> eaten 40 days ⁻¹)
12 °C Constant		0.9	22
20 °C Constant		1.4	34
26 °C Constant		1.77	43
Cool Temperature range (12 °C – 20 °C)	6:2	1.03	25
	2:2	1.15	28
	2:6	1.27	31
Warm Temperature range (20 °C – 26 °C)	6:2	1.49	36
	2:2	1.58	39
	2:6	1.67	41

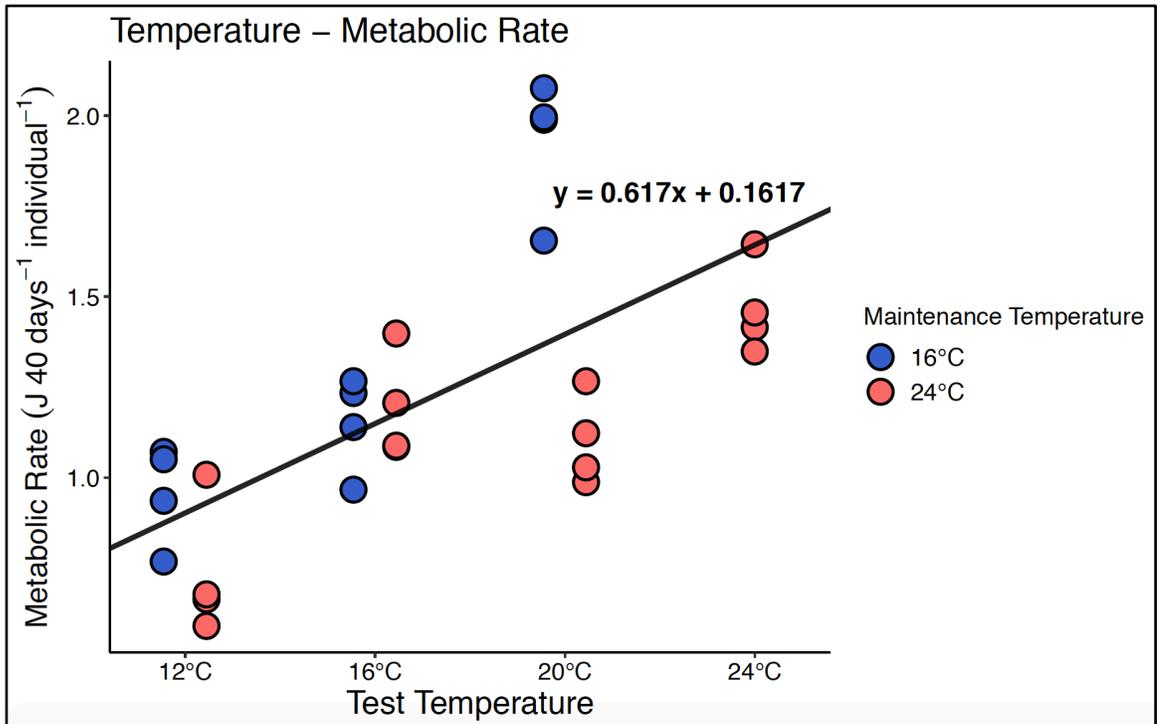


Figure 1B Temperature – metabolic rate values (derived from respirometry measurements in Chapter 2) used to estimate the metabolic demands of *S. scimitus* during the experiment. The Line of Best Fit and its equation (which was used to estimate the metabolic demands of predator mites at 12 °C constant, 20 °C constant, and 26 °C constant) are plotted.

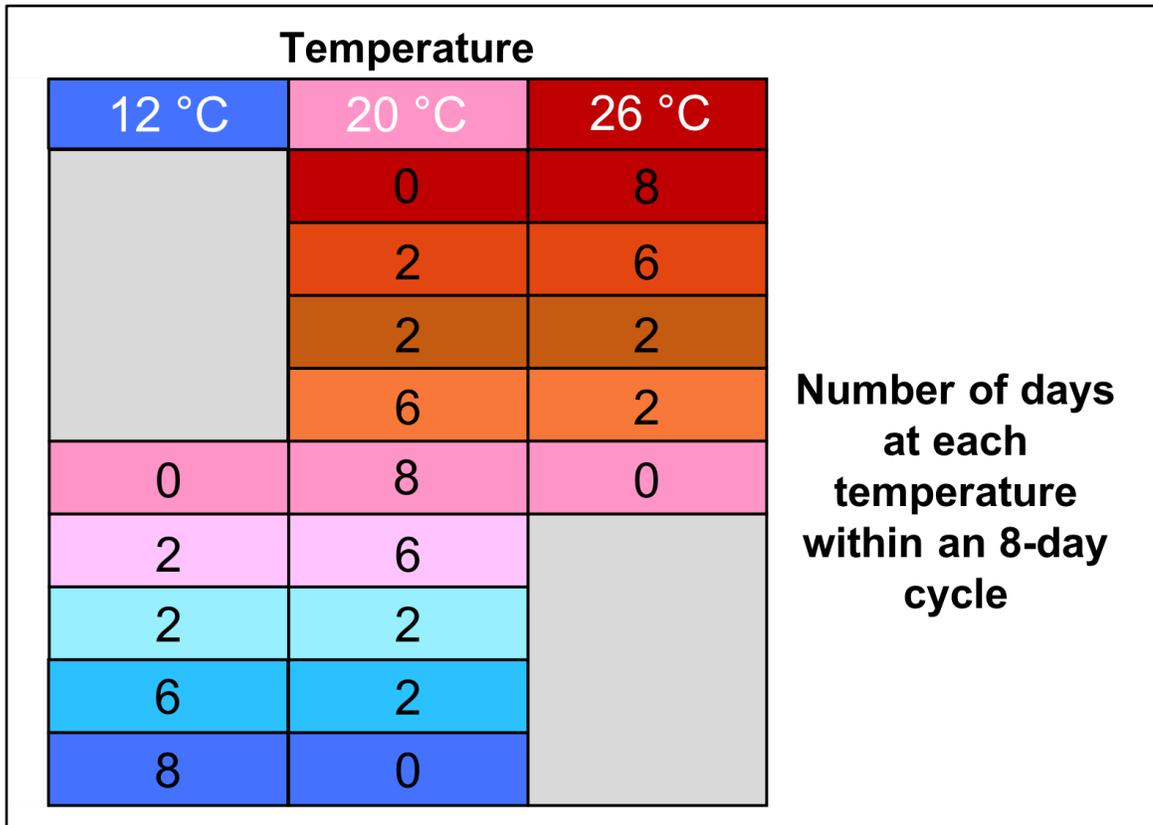


Figure 2B Conceptual diagram showing the temperature portion of the experimental design used in Chapter 3. My experiment had two temperature ranges, a cool (12 °C to 20 °C) and warm (20 °C to 26 °C) temperature range, consisting of five 8-day cycles with exposure to these temperatures. Note the overlapping treatment of 20 °C constant between the two temperature ranges. Not shown here is the predator addition treatment, where half the mesocosms received predator mites.

Mesocosm setup

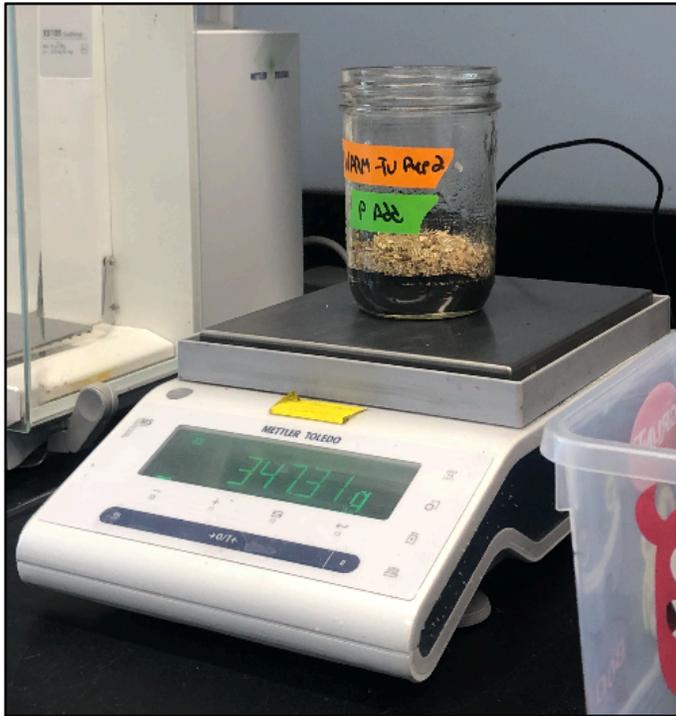


Image 1B Photograph showing the mesocosms used in Chapter 3. Mesocosms consisted of a hermetically sealed 500 ml glass mason jar, which contained a substrate of plaster of Paris and active charcoal (9:1 ratio). On top of the plaster of Paris is a layer of vermiculite to create a heterogenous environment for the predators and prey. The photograph depicts a mesocosm undergoing its weekly watering; I maintained the gravimetric moisture content by adding in water lost through evaporation every 8-days.

Appendix C Chapter 4 Supplementary Material

Table 1C Mesostigmatic species identified in this study, their average adult individual body mass (estimated, see 4.2 Methods and Materials for more details) used to calculate community weighed mean of body mass and unstandardized abundances (mean \pm SD) at each temperature, 12 °C and 20 °C.

Family	Species	Author(s), Year	Body Mass (μg)	12 °C Abundance	20 °C Abundance
Trachytidae	<i>Trachytes</i> nr. <i>lamda</i>	Berlese, 1904	22.40		0.08 \pm 0.29
Dinychidae	<i>Dinychus</i> sp.1		19.86	2.08 \pm 2.15	8.67 \pm 13.00
Dinychidae	<i>Dinychus</i> sp.2		14.05	0.33 \pm 0.65	0.75 \pm 2.30
Zerconidae	<i>Boreozercon emendi</i>	Díaz-Aguilar and Ujvári, 2010	5.92	0.58 \pm 2.02	0.17 \pm 0.58
Zerconidae	<i>Caurozercon duplex</i>	Halašková, 1977	2.85	7.50 \pm 8.59	4.00 \pm 2.52
Zerconidae	<i>Parazercon radiatus</i>	Berlese, 1910	6.84	29.33 \pm 15.33	26.33 \pm 13.64
Zerconidae	<i>Zercon</i> nr. <i>carolinensis</i>	Halašková, 1969	8.21	5.50 \pm 5.21	14.00 \pm 23.98
Zerconidae	<i>Zercon lindquisti</i>	Halašková, 1977	13.10	0.08 \pm 0.29	0.08 \pm 0.29
Veigaiidae	<i>Veigaia mitis</i>	(Berlese, 1916)	15.62	3.67 \pm 3.98	33.92 \pm 25.61
Digamasellidae	<i>Dendrolaelaps marylandae</i>	(Hurlbutt, 1967)	5.17	0.17 \pm 0.39	0.17 \pm 0.39
Ologamasidae	<i>Gamasellus vibrissatus</i>	Emberson 1967	25.19	3.67 \pm 2.9	4.75 \pm 4.39
Ologamasidae	<i>Gamasellus</i> sp.2		17.57		1.25 \pm 3.49
Parholaspididae	<i>Krantzholaspis zwartae</i>	(Marshall, 1964)	119.63	0.08 \pm 0.29	1.58 \pm 2.91
Ascidae	<i>Asca garmani</i>	Hurlbutt, 1963	4.21	2.67 \pm 1.97	6.83 \pm 7.60

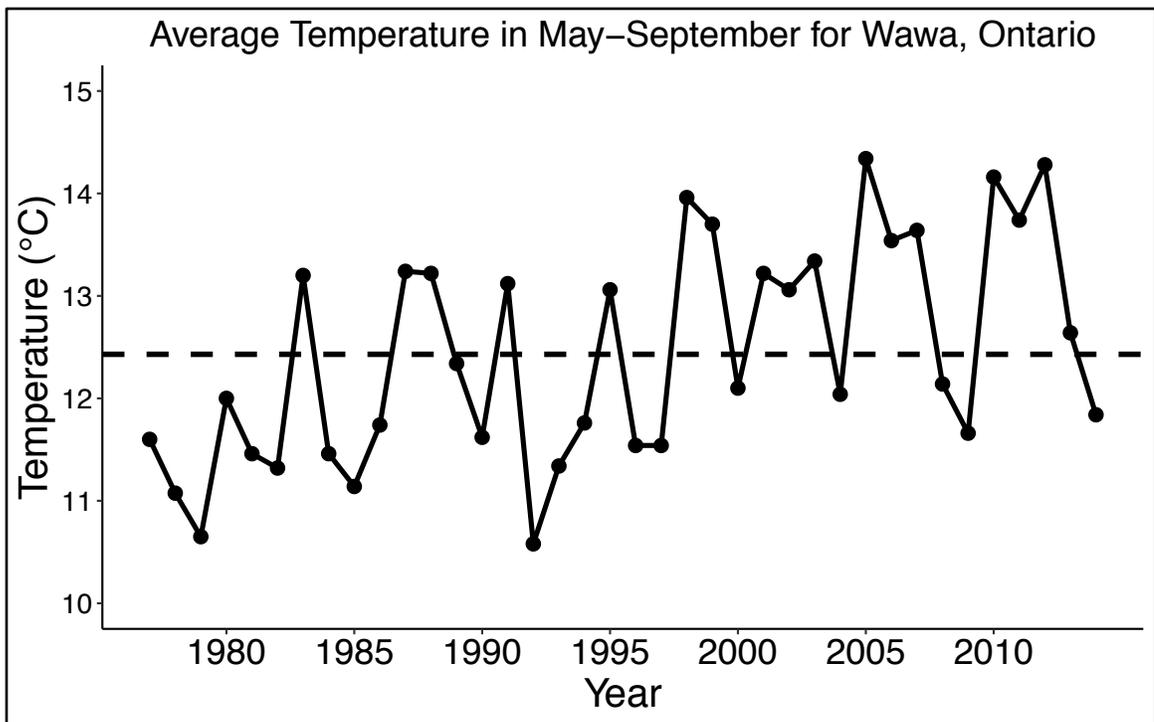


Figure 1C Growing season temperature (May – September) for Wawa Ontario (~90 km away from White River, the sampling site location) from 1977 to 2014. The dashed line indicates the average growing season (12.4 °C) during that time.



Image 1C Image showing the removal of the organic mats from the boreal forest floor. I subdivided mats into mesocosms, weighing ~155 g wet weight, into 12 °C and 20 °C incubators and were maintained for three months in complete darkness.

Curriculum Vitae

Matthew Lawrence Meehan

Post-secondary Education

Ph.D. Biology Western University London, Ontario Canada	2018 – Present
M.Sc. Biological Sciences – Specialization in Ecology University of Alberta Edmonton, Alberta, Canada	2015 – 2017
B.Sc. (Honours and Distinction) Environmental Science Western University London, Ontario Canada	2011 – 2015

Honours and Awards

- 2021 – Malcolm Ferguson Award in Life Sciences, provided by Department of Biology at Western University (value of \$1,700 CAD)
- 2021 – Invited Speaker for Graduate Student Symposium for the Entomological Society of Canada Annual Meeting (honorarium of \$200 CAD)
- 2021 – Postgraduate (Ph.D.) scholarship, provided by the Entomological Society of Canada (value of \$2,000 CAD)
- 2021 – Danks Scholarship, provided by the Entomological Society of Canada (value of \$1,500 CAD)
- 2020 – Karen Auzins Scholarship, provided by Department of Biology at Western University (value of \$1,000 CAD)
- 2019 – Winner of Best Presentation, Biology Graduate Research Forum (value of \$50 CAD)
- 2019 – Ed Becker Travel Award, provided by the Entomological Society of Canada (value of \$500 CAD)
- 2019 – Dr. Lloyd M. Dosedall Memorial Scholarship, provided by the Entomological Society of Canada (value of \$1,000 CAD)
- 2019 – Canadian Society of Ecology and Evolution Travel Award (value of \$500 CAD)
- 2019 – Science International Engagement Fund (SIEF) award, provided by the Faculty of Science at Western University (value of \$3,165 CAD)
- 2019 – Western University Biology Department Spring Travel Award (value of \$250 CAD)
- 2019 – NSERC Postgraduate Scholarship - Doctoral (PGS D, value of \$21,000 CAD x three years)
- 2019 – Ontario Graduate Scholarship (OGS, value of \$15,000 CAD) DECLINED

2018 – Runner up for Best Presentation, Ontario Ecology Ethology and Evolution Colloquium
2018 – Winner of Best Presentation, EnviroCon
2018 – Acarological Society of America Travel Award (value of \$250 US)
2017 – Letter of Commendation for Excellent Teaching for the Department of Biological Sciences at the University of Alberta
2017 – Queen Elizabeth II (QEII) Graduate Scholarship - Master's Level (value of \$5,400 CAD)
2017 – Alberta Conservation Authority Grant in Biodiversity (value of \$8,640 CAD)
2016 – University of Alberta Faculty of Graduate Studies and Research Travel Award (value of \$1,867.94 CAD)
2016 – Danks Scholarship, provided by the Entomological Society of Canada (value of \$1,000 CAD)
2015 – Western University Graduate with Distinction
2015 – Western University Dean's Honour List
2014 – Western University Dean's Honour List
2012 – Western University Dean's Honour List

Related Work Experience

Graduate Teaching Assistant: September 2015 – Present, University of Alberta (Edmonton, Alberta) and Western University (London, Ontario)

Soil Oribatida Laboratory Technician: May 2015 – August 2015, Alberta Biodiversity Monitoring Institute

Publications

†Undergraduate student mentee

Meehan, M.L., Caruso, T., Lindo, Z. 2021. Short-term intensive warming shifts predator communities (Parasitiformes: Mesostigmata) in Boreal forest soils. *Pedobiologia*. 87-88:150742.

†Ramachandran, D., Lindo, Z., **Meehan, M.L.** 2021. Predation rate and feeding efficiency in an apex soil predator under short-term reciprocal temperatures. *Basic and Applied Ecology*. 50:87-96.

Meehan, M.L., Barreto, C., Turnbull, M.S., Bradley, R.L., Bellenger, J-P., Darnajoux, R., Lindo, Z. 2020. Response of soil fauna to simulated global change factors depends on ambient climate conditions. *Pedobiologia*. 83:150672.

†Purvis, E.E.N, **Meehan, M.L.**, Lindo, Z. 2020. Agricultural field margins provide food and nesting resources to bumblebees (*Bombus* spp., Hymenoptera: Apidae) in Southwestern Ontario, Canada. *Insect Conservation and Diversity*. 13:219-228.

Meehan, M.L., Song, Z., Lumley, L.M., Cobb, T.P., Proctor, H. 2019. Soil mites as bioindicators of disturbance in the boreal forest in northern Alberta, Canada:

Testing taxonomic sufficiency at multiple taxonomic levels. *Ecological Indicators*. 102:349-365.

Meehan, M.L., Song, Z., Proctor, H. 2018. Roles of environmental and spatial factors in structuring assemblages of forest-floor Mesostigmata in the boreal region of northern Alberta, Canada. *International Journal of Acarology*. 44:300-309.

Submitted

Meehan, M.L., Turnbull, K.F., Sinclair, B.J., Lindo, Z. Predators minimize energy costs, rather than maximize energy gains under warming: Evidence from a microcosm feeding experiment. *Functional Ecology*. Accepted pending major revisions March 22, 2022. FE-2022-00058.

Meehan, M.L., Lindo, Z. Mismatches in thermal performance between ectothermic predators and prey alter interaction strength and direction. *Journal of Animal Ecology*. Submitted March 15, 2022. JAE-2022-000180.

Conference Presentations

† Undergraduate student mentee

‡ Presenter

‡**Meehan, M.L.** 2021. From individuals to communities: The effect of climate change on ectothermic predators. Graduate Student Symposium at the Annual Meeting for the Entomological Society of Canada. Online. Live Presentation.

‡**Meehan, M.L.**, Turnbull, K.F., Sinclair, B.J., Lindo, Z. 2021. Energy gains vs. losses: Warming alters predator feeding behaviour. Annual Meeting for Canadian Society of Ecology and Evolution. Online. Recorded Presentation.

‡**Meehan, M.L.**, Caruso, T., Lindo, Z. 2021. Short-term intensive warming shifts predator communities (Parasitiformes: Mesostigmata) in Boreal forest soils. Annual Meeting for Ontario Ecology Ethology and Evolution Colloquium. Online. Recorded Presentation.

Meehan, M.L., ‡Barreto, C., Turnbull, M.S., Bradley, R.L., Bellenger, J-P., Darnajoux, R., Lindo, Z. 2020. Response of soil fauna to simulated global change factors depends on ambient climate conditions. Annual Meeting for British Ecological Society. Online. Electronic Poster.

‡**Meehan, M.L.**, Caruso, T., Lindo, Z. 2020. Climate warming favours generalist predators: A case study with soil mesostigmatid (Arachnida: Mesostigmata) communities. Annual Meeting for British Ecological Society. Online. Electronic Poster.

†‡**Ramachandran, D.**, **Meehan, M.L.**, Lindo, Z. 2020. Predation rate in *Stratiolaelaps scimitus* (Womersley) (Acari: Mesostigmata) in response to short-term acclimation.

Annual Meeting for Ontario Ecology Ethology and Evolution Colloquium, Online. Recorded Presentation.

‡**Meehan, M.L.**, Turnbull, K.F., Lindo, Z. 2019. Metabolic demands on soil predators and prey selection under warm conditions. Biology Graduate Research Forum, London Ontario. Standard Talk.

‡**Meehan, M.L.**, Turnbull, K.F., Lindo, Z. 2019. Metabolic demands on soil predators and prey selection under warm conditions. Joint Meeting of Entomological Society of Canada and Canadian Society of Ecology and Evolution, Fredericton, New Brunswick. Standard Talk.

†‡**Purvis, E.E.N, Meehan, M.L.**, Lindo, Z. 2019. Agricultural field margins provide food and nesting resources to bumblebees (*Bombus* spp., Hymenoptera: Apidae) in Southwestern Ontario, Canada. Joint Meeting of Entomological Society of Canada and Canadian Society of Ecology and Evolution, Fredericton, New Brunswick. Standard Talk.

‡**Meehan, M.L.**, Barreto, C., Kustec, J, Turnbull, M.S., Bradley, R.L., Bellenger, J-P, Lindo, Z. 2018. The impact of warming on two trophic levels in microarthropod communities. Joint Meeting of Entomological Society of Canada, Entomological Society of America and Acarological Society of America, Vancouver, British Columbia. Standard Talk.

‡**Meehan, M.L.**, Barreto, C., Kustec, J, Turnbull, M.S., Bradley, R.L., Bellenger, J-P Lindo, Z. 2018. Warming rewires trophic linkages in belowground forest communities. Biology Graduate Research Forum, London Ontario. Standard Talk.

‡**Meehan, M.L.**, Kustec, J, Turnbull, M.S., Bradley, R.L., Bellenger, J-P, Lindo, Z. 2018. The effects of warming on predator-prey dynamics in soil communities. Annual Meeting for Canadian Society of Ecology and Evolution, Guelph, Ontario. Standard Talk.

‡**Meehan, M.L.**, Song, Z., Lumley, L.M., Cobb, T.P., Proctor, H. 2018. Can coarse taxonomy detect disturbance in the Boreal forest in northern Alberta? A case study with soil mites. Annual Meeting for Ontario Ecology Ethology and Evolution Colloquium, London, Ontario. Standard Talk.

‡**Meehan, M.L.**, Song, Z., Lumley, L.M., Cobb, T.P., Proctor, H. 2018. Bioindicators and ecosystem health: a case study with soil mites. EnviroCon, London, Ontario. Standard Talk.

‡**Meehan, M.L.**, Song, Z., Lumley, L.M., Cobb, T.P., Proctor, H. 2017. Assessing the relative utility of mesostigmatid mites as bioindicators of disturbance in forested areas of Alberta, Canada. R.E. Peter Biology Conference, Edmonton, Alberta. Standard Talk.

‡**Meehan, M.L.**, Song, Z., Lumley, L.M., Cobb, T.P., Proctor, H. 2017. Assessing the relative utility of mesostigmatid vs. oribatid mites as bioindicators of disturbance in forested areas of Alberta, Canada. Annual Meeting for Canadian Society of Ecology and Evolution, Victoria, British Columbia. Standard Talk.

‡**Meehan, M.L.**, Song, Z., Lumley, L.M., Cobb, T.P., Proctor, H. 2016. The effect of environmental and spatial processes on oribatid mite assemblages across provincial and regional scales in Alberta, Canada. Annual Meeting for Entomological Society of Alberta, Calgary, Alberta. Standard Talk.

‡**Meehan, M.L.**, Lindo, Z. 2016. The effect of different patch configurations of disturbance for the recolonization of mesofauna. R.E. Peter Biology Conference, Edmonton, Alberta. Standard Talk.

‡**Meehan, M.L.**, Lindo, Z. 2016. The effect of different patch configurations of disturbance for the recolonization of mesofauna. Annual Meeting for Entomological Society of Canada, Montreal, Quebec. Standard Talk.

‡**Meehan, M.L.**, Lindo, Z. 2015. The effect of different patch configurations of disturbance for the recolonization of mesofauna. Joint Biology and Environmental Science Research Day, London, Ontario. Standard Talk.

Supervision

Undergraduate Student Mentor, September 2021 – April 2022 (Student name: Eileen Reinke). Project: Assessed how acute temperature change and prey body size affect predator feeding rate and behaviour of the mite species *Stratiolaelaps scimitus*.

Undergraduate Student Mentor, September 2019 – April 2020 (Student name: Divya Ramachandran). Project: Tested how short-term acclimation affected the feeding rate and efficiency of the mite species *Stratiolaelaps scimitus*.

Undergraduate Student Mentor, September 2018 – April 2019 (Student name: Emily Purvis). Project: Analyzed and compared bumblebee diversity in agricultural field margins to semi-natural habitats.

Highschool Student Mentor, June – July 2016 (Student name: Elizabeth Chow). Project: Examined the utility of mesostigmatid mites as bioindicators of forest fire disturbance in northern Alberta.

Reviewer Activities

2022 – Experimental and Applied Acarology

2021 – Pedobiologia; Experimental and Applied Acarology; Agriculture, Environment, and Ecosystems; Proceedings B, Annals of Forest Science

2020 – Ecology and Evolution; Experimental and Applied Acarology; Forest Ecology and Management; Functional Ecology; Systematic and Applied Acarology

2019 – Pedobiologia

2018 – Écoscience; Experimental and Applied Acarology
2017 – Écoscience

Professional Experience

2021 – Organizing committee for Biology Graduate Research Forum at Western University

2018 to 2021 – Representative on the Graduate Research Committee in the Department of Biology at Western University