Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

Review

Heat stress and host–parasitoid interactions: lessons and opportunities in a changing climate

Katherine H Malinski[1], Megan Elizabeth Moore[2] and Joel G Kingsolver[1]

Ongoing climate change is increasing the frequency and magnitude of high-temperature events (HTEs), causing heat stress in parasitoids and their hosts. We argue that HTEs and heat stress should be viewed in terms of the intersecting life cycles of host and parasitoid. Recent studies illustrate how the biological consequences of a given HTE may vary dramatically depending on its timing within these lifecycles. The temperature sensitivity of host manipulation by parasitoids, and by viral endosymbionts of many parasitoids, can contribute to differing responses of hosts and parasitoids to HTEs. In some cases, these effects can result in reduced parasitoid success and increased host herbivory and may disrupt the ecological interactions between hosts and parasitoids. Because most studies to date involve endoparasitoids of aphid or lepidopteran hosts in agricultural systems, our understanding of heat responses of host–parasitoid interactions in natural systems is quite limited.

Addresses
[1] Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA
[2] Agricultural Research Service, United States Department of Agriculture, Robert W. Holley Center, 538 Tower Road, Ithaca, NY 14850, USA

Corresponding author: Kingsolver, Joel G (jgking@bio.unc.edu)

Current Opinion in Insect Science 2024, **64**:101225

This review comes from a themed issue on **Ecology**

Edited by **Renee M Borges, Radhika Venkatesan** and **Saskya van Nouhuys**

Available online 25 June 2024

https://doi.org/10.1016/j.cois.2024.101225 2214–5745/

Introduction

Climate change has intensified in the past two decades [1,2]. Recent climatic studies have highlighted the increasing frequency of extreme climatic events, including extreme precipitation and high-temperature events (HTEs; Box 1). HTEs (and other extreme events) are typically defined in terms of the frequency distribution of extreme values (e.g. daily maximum temperatures) for a given locale and the tails of that distribution [3]. For example, the frequency of daily high temperature records has increased dramatically in many regions during the past decade, and 2023 was by far the hottest year on record [4]. There are now abundant data available for heat tolerances of many insects and other ectotherms (e.g. critical thermal maximum [CT_{max}] and upper lethal thermal limit [Tu]) [5]. Similarly, there is a growing empirical literature on responses to climate change and HTEs in parasitoids and their hosts from the past decade [6–8•,9••].

HTEs in nature occur within the context of fluctuating temperatures, and the consequences of temperature fluctuations for insects have been studied extensively [10]. The differing responses of organisms to constant versus fluctuating temperatures emerge directly from the nonlinear relationship between temperature and performance (e.g. rate of survival, growth, development or reproduction), and the nonlinear effects of fluctuations are greater when they span temperatures both above and below the optimal temperature [Topt] [11]. Here, we are particularly interested in cases where the HTE includes temperatures above the optimal temperature for a population or species of interest: i.e. stressfully high temperatures.

In this review, we explore the recent literature on heat stress and host–parasitoid interactions. One central insight is that because thermal sensitivity (including heat tolerance) and microenvironmental temperatures of insects frequently differ among life stages, understanding responses to climate change requires the integration of physiological responses through the life cycle [11,12]. We propose that HTEs and heat stress should be viewed in terms of the intersecting life cycles of host and parasitoid (Figure 1), such that the biological consequences of a given HTE may vary dramatically depending on its developmental timing. As a result, HTEs can disrupt the ecological interactions between hosts and parasitoids. We describe some lessons that we have learned from summarizing this recent literature; highlight key patterns, gaps, problems, and exemplary studies associated with each lesson; and propose opportunities for future directions that address some of these gaps and outstanding questions.

Box 1 Glossary and abbreviations

Acclimation: a form of phenotypic plasticity in which exposure of an individual to environmental conditions (e.g. temperature) causes developmental or physiological changes that improve performance or fitness to subsequent environmental conditions.

CT_{max}: Critical thermal maximum or the temperature at which an organism undergoes physiological failure (often measured as muscle spasms, loss of righting behavior, or knockdown).

Heat hardening: a rapid form of thermal acclimation in which prior exposure to heat increases survival of an individual to stressful high temperatures.

HTE: high-temperature event, for example, heat wave or heat shock.

Idiobiont: parasitoid that permanently paralyzes and halts development of its host.

Koinobiont: a parasitoid that allows its host to continue development after parasitization.

Parasitoid: an insect that completes its larval development within or on the body of another insect eventually killing it and is free-living as an adult.

PDV: Vertically inherited virus-like entities (also called viriforms) from the family Polydnaviridae that are endogenized in the genomes of ichneumonid and braconid wasps. Produce virion-like particles that do not contain the necessary mechanisms for viral replication. These virion-like particles encapsidate parasitoid DNA that is injected into the host during oviposition and serve as a template for parasitoid proteins that perform important functions in host manipulation such as immune suppression and hormone modulation (adapted from Ref. [81]).

Teratocyte: Parasitoid cells released into hosts when parasitoid eggs hatch. Function in the disruption of host metamorphosis by reducing host juvenile hormone esterase (JHE) levels, though some evidence suggests they also function in immune evasion and damage of host cells to release nutrients for developing parasitoid larvae. Produced by Braconidae of the microgastroid complex and Platygastroidea (adapted from Ref. [82]).

Thermal mismatch: Phenomena when the thermal tolerances of the host organism and the parasitoid differ; this can change across the ontogeny of both host and parasitoid, as thermal tolerance is not static (e.g. the CT_{max} of the host is higher than the CT_{max} of the parasitoid).

Thermal safety margin: The difference between the maximum environmental temperature and an organism's CT_{max}.

Topt: Optimal temperature or the temperature at which an organismal trait is at its highest possible performance (e.g. walking speed, flight capacity, host handling).

Tu: Upper lethal thermal limit or the temperature at which an organism dies.

Lesson 1: *Most data are from agricultural pest hosts and hymenopteran endoparasitoids that develop inside of the living host (koinobionts).*

We summarized empirical studies of heat tolerance and HTE responses in parasitoids and their hosts published between 2014 and 2023 [7,13–62]. More than 90% of studies involved hosts that are agricultural pests, primarily Lepidoptera and aphids. More than 75% of the parasitoids (all endoparasitoids that develop inside the host) attack larval or nymphal host stages (Figure 1B, C); and more than 50% of the studies involve braconid or aphilinid parasitoids. Given the enormous diversity of parasitoids and of parasitoid life histories [63], our general understanding of heat stress and host–parasitoid interactions will be strongly limited by the habitat, taxonomic, and life history biases of the current literature (but see Ref. [61••] for a notable exception]. The majority of these studies involve lab assays of heat tolerance or lab experimental manipulations of heat shocks, heat waves, or developmental temperatures, but a handful of recent studies explore heat responses in field conditions [17,23,36••,60,62].

Opportunities: *Studies of parasitoids in natural (non-managed) systems and those that represent the phylogenetic diversity of parasitoids and hosts are needed. Studies that combine laboratory and field approaches may be particularly valuable for understanding parasitoid heat tolerance and its ecological consequences.*

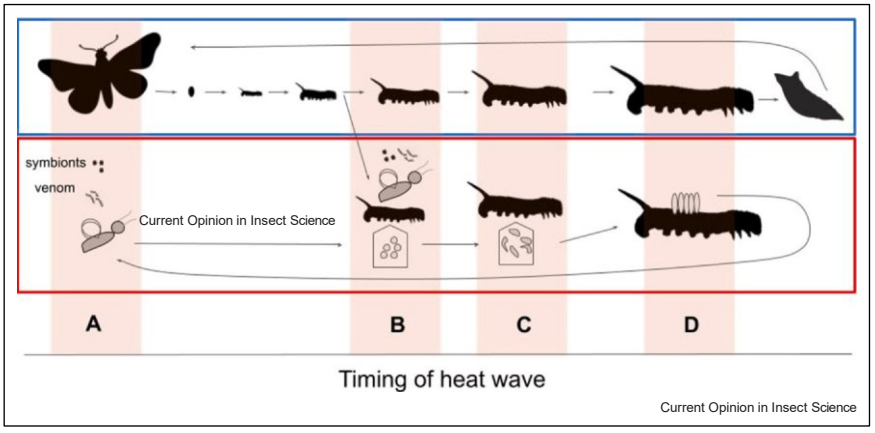
Lesson 2: *The parasitoid life stage at which high-temperature events (HTEs) occur is crucial in determining the outcomes of the host/parasitoid interactions.*

Parasitoid success relies on physiological mechanisms intrinsically tied to their own development and that of their hosts, which can be disrupted by HTEs [34,55•,63]. Thermal tolerance is not constant across development; the timing of HTEs, in terms of both host and parasitoid development, can dictate parasitoid success or failure [27,55•,64] (Figure 1).

Adult: Numerous studies show that HTEs in adult parasitoids can reduce survival, female activity, or oviposition success [14,39•,51,65]. Adult exposure to HTEs can also negatively impact offspring performance (development, emergence, survival, and parasitism success) via transgenerational effects [48,65].

Pupal: The pupal stage of insects is a complex dance of precisely timed developmental events necessary for metamorphosis into adults. Several studies demonstrated that the pupal stage can exhibit increased thermal sensitivity to HTEs, resulting in decreased adult longevity, fecundity, and survival to adult eclosion

Figure 1



Graphical depiction of the interconnected life cycles of a parasitoid (red box) and its host (blue box), in relation to the timing of a heat wave (shaded pink regions). A gregarious larval koinobiont of a lepidopteran host is shown here as an illustration, but effects of HTEs on host and parasitoid can be generalized across other types of parasitoids (e.g. egg, solitary, etc.). HTEs can have important, divergent consequences for free-living versus independent parasitoid life stages. All parasitoids are typically free-living in the adult stage (A). The pupal stage (D) can also be free-living, but some parasitoid species remain attached to the host during pupation and manipulate host behavior to defend cocoons. The parasitoid is dependent upon the host body for egg (B) and larval (C) life stages, with distinct differences in life history traits at each stage. For endoparasitoid koinobionts, both life stages must ensure the internal host environment is hospitable for developing parasitoids, for example, via immunosuppression or developmental disruption of the host by venom or symbionts. Egg stages (B) are stationary and have limited energetic reserves, while larval stages (C) can be motile, able to feed, and are sometimes accompanied by specialized teratocyte cells, which aid in host manipulation. Because of these life cycle complexities, the fitness consequences of an HTE depend critically on its developmental timing.

[34,48]. In many insects, sperm development and maturation occur during pupation [66]. Sperm quantity in male seminal vesicles can decrease with heat stress, for example, in both *Microplitis rufiventris* and *Cotesia typhae parasitoids*, with the latter also displaying decreased sperm storage in mated females [42,58••].

Egg/larval: HTEs can negatively impact egg parasitoids [17], and multiple studies have shown detrimental effects of high-temperature stress throughout parasitoid larval development [19,45,67]. Some parasitoid larval instars may be more sensitive to thermal stress than others, so the timing and duration of HTEs also contribute to their impacts on parasitoid success (see Lesson 4) [34,55•]. There is also evidence that, unlike many insects, some parasitoids do not exhibit heat hardening during larval development, while their hosts do [68•].

These studies demonstrate how heat stress can reduce parasitoid fitness across multiple metrics and life stages, and these effects depend on the developmental timing of HTEs. However, the general importance of heat acclimation in different parasitoid species and life stages remains unclear [27,53,68•].

Opportunities: *Most evidence of thermal tolerance across ontogeny comes from limited systems and taxa and focuses on singular life stages. Further exploration of how past temperature exposure, acclimation, and transgenerational effects impact host–parasitoid interactions across ontogeny will be necessary for understanding the effects of HTEs beyond the organismal level.*

Lesson 3: *Viral endosymbionts, venom, and other host manipulation adaptations can limit the thermal tolerance of parasitoids.*

Parasitoid death can result from the direct effects of high-temperature stress or indirectly from the disruption of their host manipulation mechanisms, which can complicate studies measuring CT_{max} or thermal limits of parasitic life stages. Experiments that differentiate between these distinct mechanisms of parasitoid death inside hosts at high temperatures are rare but useful for understanding the physiological and organismal drivers of parasitoid thermal tolerance, particularly for important biocontrol species. Here, we discuss recent literature concerning the impact of HTEs on parasitoid strategies for manipulation of hosts. Parasitoids often rely on highly specialized adaptations that allow for immobilization, immunosuppression, or other manipulation of the host body for successful reproduction [69–72]. Many of these adaptations involve temperature-dependent physiological reactions, which can be altered under HTEs. For example, endoparasitoids often use venom to subdue host mobility, immunity, or other aspects of their physiology and behavior [72]. Several recent studies document climatic gradients or effects of HTEs in

venom composition [41]. However, little is known about temperature effects on parasitoid venom function in host manipulation and parasitoid fitness.

Endosymbionts, such as polydnaviruses (PDVs), are another important parasitoid adaptation for successful parasitism of hosts. PDVs function as gene delivery vehicles, allowing for expression of virulence genes used in host immunosuppression, altered development, and behavioral manipulation [69,72]. Several recent studies demonstrated HTEs altered PDV function, resulting in less effective suppression of host immune responses and increased (sometimes complete) parasitoid mortality [21,45,55•,59]. These patterns suggest PDVs and potentially other symbionts can limit the thermal tolerance of some parasitoids, though the generality of these patterns remains unknown (but see discussion of facultative symbionts in Lesson 5).

Recent work also suggests HTEs can affect parasitoid physiology directly. Several studies demonstrate that parasitoids respond to heat stress via production of key antioxidant enzymes (superoxide dismutase, catalase, peroxidase, and glutathione-S-transferase) [47,54••,67]; these enzymes increased resistance of parasitoids to high temperatures [54••].

For koinobionts, parasitoid development is interconnected with that of the host (Figure 1). Parasitoids often disrupt hormones to manipulate host development [73], but the effect of HTEs on hormonal manipulation has, to our knowledge, not been previously examined. Likewise, teratocytes are important parasitoid cells, which aid in the disruption of host metamorphosis [74], but the impacts of HTEs on teratocyte function, or their interactions with venom and PDVs, have not been investigated.

Opportunities: *The impact of HTEs on mechanisms of host manipulation is largely unknown for the vast majority of parasitoid species. Further research is needed to determine how hormones, teratocytes, and venom mediate interactions with the host across thermal regimes and whether reduced PDV function at high temperatures is a generalizable effect across diverse parasitoid taxa which rely on these endosymbionts.*

Lesson 4: *Thermal mismatches in heat tolerance between hosts and parasitoids are common but not universal*.

Differences in thermal sensitivity between interacting species — 'thermal mismatches' — are critical ecological responses to climate change. Thermal mismatch at lower temperatures can cause phenological shifts between interacting species, including hosts and parasitoids [75]. At higher environmental temperatures, differences in optimal temperature (Topt) and heat tolerance between hosts and parasitoids can similarly generate different fitness consequences of climate warming and HTEs [6,8•]. Multiple studies have documented that heat tolerance (CT_{max} or heat knockdown time) is lower for adult parasitoids than for their (unparasitized) hosts in a number of systems [24,26,27,29,61••].

One limitation of these studies is that CT_{max} is generally measured for adult parasitoids in relation to adult or larval hosts; heat tolerance of the parasitoid itself, or parasitoid's mechanisms of host control (venom, endosymbiont), may be limiting in other parasitoid life stages (Figure 1), and adult parasitoids have greater potential opportunity to avoid deleterious high temperatures by microhabitat selection. More generally, the difference between maximum environmental temperature and CT_{max} (thermal safety margin) is often more than 10°C for most insects, including parasitoids [5,61••], so the ecological significance of small differences in CT_{max} is unclear. Additionally, CT_{max} is generally unknown for other parasitoid life stages (but see Ref. [55•]), and whether high temperatures are limiting for the parasitoid or their endosymbionts, or both, will likely be species dependent.

An alternative approach is to use experimental heat shocks or heat waves on parasitized hosts to explore contrasting effects on host and parasitoid success [19,25,34,42,44,45]. These studies demonstrate HTEs generally reduce parasitoid fitness, but the magnitude of these effects can vary with their number, intensity, and development timing. Heat stress of larval parasitoids can also negatively impact adult survival, fertility, and fecundity [19,34,42,58••], and heat stress of adult parasitoids can reduce offspring fitness [48,65]. It is clear that HTEs negatively impact parasitoid fitness, but the variability in timing of HTEs, and their magnitude/duration, render quantification and comparison of these results more difficult.

Unsurprisingly, heat stress frequently reduces survival of parasitized hosts, but there are noteworthy exceptions. For example, several studies showed that parasitism conferred increased resistance to heat shock [30,68] likely because parasitism can elicit stress responses in hosts (see Lesson 3). Several studies demonstrated HTEs facilitated clearing of parasitoids and increased host survival [20,59]. Further exploration of the fitness benefits of heat stress on parasitized hosts is warranted.

The ecological relevance of thermal mismatches depends critically on the body temperatures of host and parasitoids in field conditions. Microclimates and insect temperatures can differ dramatically from ambient air temperatures, especially at higher temperatures [76,77]. The few studies that quantify microclimate variation or operative (body) temperatures in the field suggest stressful sublethal and lethal high temperatures can occur regularly in both tropical and temperate systems [26,40,60], and that

microclimatic variation may be associated with variation in levels of parasitism and herbivory. In addition, the relative importance of heat stress and water loss in adult parasitoids in the field is largely unknown, but likely a key limiting factor for parasitoid success.

Opportunities: *Applying the concept of 'thermal mismatch' to specific host and parasitoid life stages will be fruitful. The potential fitness benefits of heat stress for parasitized hosts require further exploration. Data on microclimate variation and operative temperatures of hosts and parasitoids across their lifecycles in the field are sorely needed to evaluate the ecological relevance of heat tolerance, and to inform landscape management plans.*

Lesson 5: *HTEs can destabilize host–parasitoid interactions, thereby increasing herbivory of insect pests* via *reduced top-down control under climate change*.

The developmental outcomes of host–parasitoid interactions can have important implications for broader ecological networks. For example, HTEs increased herbivory levels fourfold in a hostplant–host–parasitoid system, driven by parasitoid failure to kill hosts at high temperatures [62]. HTEs and climate change can also alter the competitive outcomes of intraspecific parasitoid–parasitoid interactions [7,56•].

Recent work (primarily in aphids) highlights the important role of microbial symbionts in mediating insect thermal tolerances and interactions between hosts and parasitoids. For various aphid species, infection with bacteria [57] or viruses [38] increased survival or fecundity in response to HTEs [57]. In some cases, symbionts can confer host resistance to parasitoids, while heat stress generally lowers this protection; the overall adaptive benefit of hosting symbionts is greater under high temperatures than nonstressful temperatures [57]. Fitness consequences of microbial associations in non-aphid hosts and in parasitoids are understudied, but the evidence that facultative symbionts can limit or expand thermal tolerances in diverse insect taxa is substantial (reviewed in Ref. [78]), which suggests facultative symbionts are likely important mediators of parasitoid thermal tolerance.

Meta-analyses and large-scale field surveys have been particularly important for assessing the effects of HTEs on host–parasitoid outcomes and their cascading ecological consequences. These studies demonstrate a common result of HTEs generally reducing parasitoid prevalence or success, resulting in increased herbivory of hostplants [17,36••,56•,61••]. Conversely, warm summers in the arctic increased parasitism of Dipteran hosts, resulting in reduced Dipteran pollination of plants [36••]. This suggests that the effects of climate change on parasitoids may differ across climate regions, and host taxa could be differentially impacted by climate change, yielding different types of cascading ecological responses; more research is needed to explore and characterize these effects.

Models that incorporate data from both lab studies and field surveys are particularly valuable for understanding how HTEs may alter ecological dynamics. A model for aphid–parasitoid abundances predicted HTEs lead to shortened and intensified host–parasitoid population cycling, resulting in destabilized host–parasitoid dynamics [13]. Several other models predict that climate warming will decrease the stability of herbivore food webs [61••]. Combined, these models and field surveys agree with a growing body of research suggesting HTEs disrupt host–parasitoid species networks, and herbivory of agricultural and natural hostplants is expected to increase under climate change as top-down control of insect pests is relaxed [79].

Opportunities: *Empirical studies examining the effects of temperature on host–parasitoid dynamics and their multitrophic interactions with other species are incredibly valuable, but rare, especially in non-managed systems. While such studies are logistically challenging, they are an ideal staging ground for integrative and collaborative research across fields.*

The field of host–parasitoid thermal biology has expanded in scope in the past decade. Our understanding, which comes primarily from agricultural systems, indicates that high-temperature stress can disrupt parasitoid control of host insects, but this is highly dependent on both host and parasitoid life stage, and can be moderated by physiological mechanisms of host control. We have seen that with a few notable exceptions, host thermal tolerance exceeds that of their parasitoids, resulting in cascading trophic effects. Future studies should expand into non-agricultural systems and non-laboratory settings, investigate effects beyond the organismal level, and incorporate modeling approaches to produce generalizable predictions. These areas provide rich opportunities for novel, integrative research, and collaboration across scientific fields.

Funding

Research supported in part by National Science Foundation, USA. Grant no. IOS-2029156 to JGK.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could

have appeared to influence the work reported in this paper.

Acknowledgements

Thanks to Greg Biddle for proofreading and assessing definitions and abbreviations.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Intergovernmental Panel On Climate Change (Ipcc): **Climate Change 2022 — Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change**. Cambridge University Press; 2023.
2. Harvey JA, Tougeron K, Gols R, Heinen R, Abarca M, Abram PK, Basset Y, Berg M, Boggs C, Brodeur J, *et al.*: **Scientists' warning on climate change and insects**. *Ecol Monogr* 2023, **93**:e1553.
3. Kingsolver JG, Buckley LB: **Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate**. *Philos Trans R Soc B Biol Sci* 2017, **372**:20160147.
4. NOAA: **Earth Had Its Warmest Year on Record; Upper-Ocean Heat Content Was Record High While Antarctic Sea Ice Was Record Low**; 2024.
5. Weaving H, Terblanche JS, Pottier P, English S: **Meta-analysis reveals weak but pervasive plasticity in insect thermal limits**. *Nat Commun* 2022, **13**:5292.
6. Furlong MJ, Zalucki MP: **Climate change and biological control: the consequences of increasing temperatures on host-parasitoid interactions**. *Curr Opin Insect Sci* 2017, **20**:39-44.
7. Costaz TPM, de Jong PW, Harvey JA, van Loon JJA, Dicke M, Gols R: **Temperature affects the outcome of competition between two sympatric endoparasitoids**. *Anim Behav* 2023, **203**:11-20.
8. • Le Lann C, van Baaren J, Visser B: **Dealing with predictable and unpredictable temperatures in a climate change context: the case of parasitoids and their hosts**. *J Exp Biol* 2021, **224**:jeb238626.

A review paper investigating the evolutionary strategies of parasitoids and their host insects when experiencing fluctuating environments that are either predictable or not, which provides a robust framework for future experiments.

9. •• Costaz TPM, de Jong PW, van Loon JJA, Dicke M: **It is about time: effects of thermal fluctuations resulting from climate change on trophic interactions with a focus on host–parasitoid interactions**. *Evol Ecol* 2023, **37**:601-625.

A thorough and robust review of the effects of fluctuating temperatures on host–parasitoid interactions and their broader multitrophic effects, ranging across biological scales from molecular to ecological. A necessary read for an overview of the field of thermal biology in hos- t–parasitoid systems.

10. Colinet H, Sinclair BJ, Vernon P, Renault D: **Insects in fluctuating thermal environments**. *Annu Rev Entomol* 2015, **60**:123-140.
11. Buckley LB, Kingsolver JG: **Evolution of thermal sensitivity in changing and variable climates**. *Annu Rev Ecol Evol Syst* 2021, **52**:563-586.
12. Johnson CA, Ren R, Buckley LB: **Temperature sensitivity of fitness components across life cycles drives insect responses to climate change**. *Am Nat* 2023, **202**:753-766.
13. Meisner MH, Harmon JP, Ives AR: **Temperature effects on long-term population dynamics in a parasitoid–host system**. *Ecol Monogr* 2014, **84**:457-476.
14. Jerbi-Elayed M, Lebdi-Grissa K, Le Goff G, Hance T: **Influence of temperature on flight, walking and oviposition capacities of two aphid parasitoid species (Hymenoptera: Aphidiinae)**. *J Insect Behav* 2015, **28**:157-166.
15. Moiroux J, Boivin G, Brodeur J: **Temperature influences host instar selection in an aphid parasitoid: support for the relative fitness rule**. *Biol J Linn Soc* 2015, **115**:792-801.
16. Moiroux J, Abram PK, Louâpre P, Barrette M, Brodeur J, Boivin G: **Influence of temperature on patch residence time in parasitoids: physiological and behavioural mechanisms**. *Sci Nat* 2016, **103**:32.
17. Wu L-H, Hoffmann AA, Thomson LJ: **Potential impact of climate change on parasitism efficiency of egg parasitoids: a meta-analysis of *Trichogramma* under variable climate conditions**. *Agric Ecosyst Environ* 2016, **231**:143-155.
18. Alford L, Kishani Farahani H, Pierre J-S, Burel F, van Baaren J: **Why is there no impact of the host species on the cold tolerance of a generalist parasitoid?** *J Insect Physiol* 2017, **103**:71-77.
19. Schreven SJJ, Frago E, Stens A, de Jong PW, van Loon JJA: **Contrasting effects of heat pulses on different trophic levels, an experiment with a herbivore-parasitoid model system**. *PLoS One* 2017, **12**:e0176704.
20. Seehausen ML, Régnière J, Martel V, Smith SM: **Developmental and reproductive responses of the spruce budworm (Lepidoptera: Tortricidae) parasitoid *Tranosema rostrale* (Hymenoptera: Ichneumonidae) to temperature**. *J Insect Physiol* 2017, **98**:38-46.
21. Seehausen ML, Cusson M, Régnière J, Bory M, Stewart D, Djoumad A, Smith SM, Martel V: **High temperature induces downregulation of polydnavirus gene transcription in lepidopteran host and enhances accumulation of host immunity gene transcripts**. *J Insect Physiol* 2017, **98**:126-133.
22. Wetherington MT, Jennings DE, Shrewsbury PM, Duan JJ: **Climate variation alters the synchrony of host–parasitoid interactions**. *Ecol Evol* 2017, **7**:8578-8587.
23. Abarca M, Lill JT, Frank-Bolton P: **Latitudinal variation in responses of a forest herbivore and its egg parasitoids to experimental warming**. *Oecologia* 2018, **186**:869-881.
24. Agosta SJ, Joshi KA, Kester KM: **Upper thermal limits differ among and within component species in a tritrophic host-parasitoid-hyperparasitoid system**. *PLoS One* 2018, **13**:e0198803.
25. Iltis C, Martel G, Thiéry D, Moreau J, Louâpre P: **When warmer means weaker: high temperatures reduce behavioural and immune defences of the larvae of a major grapevine pest**. *J Pest Sci* 2018, **91**:1315-1326.
26. Machekano H, Mvumi BM, Nyamukondiwa C: **Loss of coevolved basal and plastic responses to temperature may underlie trophic level host-parasitoid interactions under global change**. *Biol Control* 2018, **118**:44-54.
27. Mutamiswa R, Chidawanyika F, Nyamukondiwa C: **Thermal plasticity potentially mediates the interaction between host *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) and endoparasitoid *Cotesia flavipe*s Cameron (Hymenoptera: Braconidae) in rapidly changing environments**. *Pest Manag Sci* 2018, **74**:1335-1345.
28. Mutamiswa R, Machekano H, Chidawanyika F, Nyamukondiwa C: **Thermal resilience may shape population abundance of two sympatric congeneric Cotesia species (Hymenoptera: Braconidae)**. *PLoS One* 2018, **13**:e0191840.
29. Mutamiswa R, Chidawanyika F, Nyamukondiwa C: **Comparative assessment of the thermal tolerance of spotted stemborer, Chilo partellus (Lepidoptera: Crambidae) and its larval parasitoid, Cotesia sesamiae (Hymenoptera: Braconidae)**. *Insect Sci* 2018, **25**:847-860.
30. Trotta V, Forlano P, Falabella P, Battaglia D, Fanti P: **The aphid *Acyrthosiphon pisum* exhibits a greater survival after a heat shock when parasitized by the wasp *Aphidius ervi***. *J Therm Biol* 2018, **72**:53-58.
31. Wang X-G, Serrato MA, Son Y, Walton VM, Hogg BN, Daane KM: **Thermal performance of two indigenous pupal parasitoids**

attacking the invasive *Drosophila suzukii* (Diptera: Drosophilidae). *Environ Entomol* 2018, **47**:764-772.

32. Castellanos NL, Bueno AF, Haddi K, Silveira EC, Rodrigues HS, Hirose E, Smagghe G, Oliveira EE: **The fitness and economic benefits of rearing the parasitoid *Telenomus podisi* under fluctuating temperature regime**. *Neotrop Entomol* 2019, **48**:934-948.

33. Mathé-Hubert H, Kremmer L, Colinet D, Gatti J-L, Van Baaren J, Delava É, Poirié M: **Variation in the venom of parasitic wasps, drift, or selection? Insights from a multivariate QST analysis**. *Front Ecol Evol* 2019, **7**.

34. Zhang Y-B, Zhang G-F, Liu W-X, Wan F-H: **Continuous heat waves change the life history of a host-feeding parasitoid**. *Biol Control* 2019, **135**:57-65.

35. Iltis C, Moreau J, Manière C, Thiéry D, Delbac L, Louâpre P: **Where you come from matters: temperature influences host–parasitoid interaction through parental effects**. *Oecologia* 2020, **192**:853-863.

36. •• Kankaanpää T, Vesterinen E, Hardwick B, Schmidt NM, Andersson T, Aspholm PE, Barrio IC, Beckers N, Bêty J, Birkemoe T, *et al.*: **Parasitoids indicate major climate-induced shifts in arctic communities**. *Glob Change Biol* 2020, **26**:6276-6295.

An impressive study in ecological and geographical scale examining an understudied biome in the parasitoid literature (the arctic). Outstanding in its standardized sampling across multiple locations in different countries, the inclusion of two parasitoid orders and a broad community assembly of host taxa and the inclusion of multitrophic interactions with an important arctic plant family.

37. Moore ME, Kester KM, Kingsolver JG: **Rearing temperature and parasitoid load determine host and parasitoid performance in *Manduca sexta* and *Cotesia congregata***. *Ecol Entomol* 2020, **45**:79-89.

38. Porras MF, Navas CA, Marden JH, Mescher MC, De Moraes CM, Pincebourde S, Sandoval-Mojica A, Raygoza-Garay JA, Holguin GA, Rajotte EG, *et al.*: **Enhanced heat tolerance of viral-infected aphids leads to niche expansion and reduced interspecific competition**. *Nat Commun* 2020, **11**:1184.

39. • Valls A, Kral-O'Brien K, Kopco J, Harmon JP: **Timing alters how a heat shock affects a host-parasitoid interaction**. *J Therm Biol* 2020, **90**:102596.

An empirical study that emphasizes the importance of precise timing of heat shocks, showing that parasitism success is moderated through adult female behavior during stressfully high temperatures in an aphid-parasitoid system.

40. Bernaschini ML, Rossetti MR, Valladares G, Salvo A: **Microclimatic edge effects in a fragmented forest: disentangling the drivers of ecological processes in plant-leafminer-parasitoid food webs**. *Ecol Entomol* 2021, **46**:1047-1058.

41. Cavigliasso F, Gatti J-L, Colinet D, Poirié M: **Impact of temperature on the immune interaction between a parasitoid wasp and drosophila host species**. *Insects* 2021, **12**:647.

42. El-Sabrout AM, Hegazi E, Khafagi W, Bressac C: **Sperm production is reduced after a heatwave at the pupal stage in the males of the parasitoid wasp *Microplitis rufiventris* Kok (Hymenoptera; Braconidae)**. *Insects* 2021, **12**:862.

43. Ion Scotta M, Margris L, Sellier N, Warot S, Gatti F, Siccardi F, Gibert P, Vercken E, Ris N: **Genetic variability, population differentiation, and correlations for thermal tolerance indices in the minute wasp, *Trichogramma cacoeciae***. *Insects* 2021, **12**:1013.

44. Jerbi-Elayed M, Foray V, Tougeron K, Grissa-Lebdi K, Hance T: **Developmental Temperature affects life-history traits and heat tolerance in the Aphid parasitoid *Aphidius colemani***. *Insects* 2021, **12**:852.

45. Moore ME, Hill CA, Kingsolver JG: **Differing thermal sensitivities in a host–parasitoid interaction: high, fluctuating developmental temperatures produce dead wasps and giant caterpillars**. *Funct Ecol* 2021, **35**:675-685.

46. Schoeller EN, Redak RA: **The effects of temperature and host stage on development rate of parasitoids of giant whitefly *Aleurodicus dugesii* (Hemiptera: Aleyrodidae)**. *Environ Entomol* 2021, **50**:192-201.

47. Shankarganesh K, Selvi C, Karpagam C: **Effects of thermal stress on the antioxidant defenses in Paracoccus marginatus Williams and Granara de Willink parasitized by Acerophagus papayae Noyes & Schauff**. *Int J Trop Insect Sci* 2021, **41**:433-438.

48. Simaz O, Szűcs M: **Heat waves affect an invasive herbivore and its parasitoid differentially with impacts beyond the first generation**. *Ecosphere* 2021, **12**:e03796.

49. Smith AH, O'Connor MP, Deal B, Kotzer C, Lee A, Wagner B, Joffe J, Woloszynek S, Oliver KM, Russell JA: **Does getting defensive get you anywhere?—Seasonal balancing selection, temperature, and parasitoids shape real-world, protective endosymbiont dynamics in the pea aphid**. *Mol Ecol* 2021, **30**:2449-2472.

50. Chen L, Sørensen JG, Enkegaard A: **Acclimation for optimisation: effects of temperature on development, reproduction and size of *Trichogramma achaeae***. *Biocontrol Sci Technol* 2022, **32**:60-73.

51. Costaz TPM, Gols R, de Jong PW, van Loon JJA, Dicke M: **Effects of extreme temperature events on the parasitism performance of *Diadegma semiclausum*, an endoparasitoid of Plutella xylostella**. *Entomol Exp Appl* 2022, **170**:656-665.

52. Ismail M, Tougeron K, Vriamont A, Hance T, Albittar L: **Thermal tolerance of the rosy apple aphid *Dysaphis plantaginea* and its parasitoids: effect of low temperatures on some fitness activities of Aphidius matricariae**. *J Therm Biol* 2022, **110**:103377.

53. Jerbi-Elayed M, Tougeron K, Grissa-Lebdi K, Hance T: **Effect of developmental temperatures on *Aphidius colemani* host-foraging behavior at high temperature**. *J Therm Biol* 2022, **103**:103140.

54. • Liu X, Fu Z-X, Kang Z-W, Li H, Liu T-X, Wang D: **Identification and characterization of antioxidant enzyme genes in parasitoid *Aphelinus asychis* (Hymenoptera: Aphelinidae) and expression profiling analysis under temperature stress**. *Insects* 2022, **13**:447.

A lab experiment that demonstrated antioxidant enzyme genes are upregulated by high-temperature stress in an agriculturally important aphid parasitoid. Female parasitoids had a higher thermal tolerance than males and also expressed these genes at higher levels in response to heat. These results suggest antioxidant enzymes confer tolerance of parasitoids to high temperature extremes.

55. • Moore ME, Hill CA, Kingsolver JG: **Developmental timing of extreme temperature events (heat waves) disrupts host–parasitoid interactions**. *Ecol Evol* 2022, **12**:e8618.

An experimental study that demonstrates heat waves and heat shocks of parasitized hosts can result in very different fitness outcomes for hosts and parasitoids depending on the developmental timing of heat stress. One intriguing finding is that heat stress soon after parasitization can result in complete mortality of parasitoids and the generation of giant, long-lived host larvae.

56. • Pardikes NA, Revilla TA, Lue C-H, Thierry M, Souto-Vilarós D, Hrcek J: **Effects of phenological mismatch under warming are modified by community context**. *Glob Change Biol* 2022, **28**:4013-4026.

A combined approach of laboratory experiments and simulations, which show that warming decreases the window of host susceptibility to parasitoid attack. Presence of an alternative host species allowed for sustained parasitoid presence despite phenological shifts in the window of host availability, but the reduced performance of parasitoids under warming may negate community assemblage effects

57. Tougeron K, Iltis C: **Impact of heat stress on the fitness outcomes of symbiotic infection in aphids: a meta-analysis**. *Proc R Soc B Biol Sci* 2022, **289**:20212660.

58. •• Bressac C, El Sabrout A, Kifouche F, Anne M, Capdevielle-Dulac C, Mougel F, Kaiser L: **Hot and cold waves decrease sperm production and bias sex ratio in the parasitoid wasp *Cotesia typhae* (Hymenoptera, Braconidae)**. *J Insect Physiol* 2023, **149**:104553.

A multilevel examination of the effects of high- and low-temperature stress during pupation on male sperm development, female storage of

sperm, and the sex ratio of offspring, which has important implications for haplodiploid parasitoids like Hymenoptera.

59. Malinski KH, Sorenson CE, Moore ME, Willett CS, Kingsolver JG: **Host species differences in the thermal mismatch of host–parasitoid interactions**. *J Exp Biol* 2023, **226**:jeb245702.

60. Moore ME, Alston MA, Kingsolver JG: **Behavioral thermoregulation of caterpillars is altered by temperature, but not parasitism: an empirical field study**. *Ecosphere* 2023, **14**:e4578.

61. •• Wenda C, Gaitán-Espitia JD, Solano-Iguaran JJ, Nakamura A, Majcher BM, Ashton LA: **Heat tolerance variation reveals vulnerability of tropical herbivore–parasitoid interactions to climate change**. *Ecol Lett* 2023, **26**:278-290.

A robust ecological study across host and parasitoid community assemblages in two tropical niches with different thermal regimes. The results support the general understanding that parasitoids often have lower heat tolerance than their hosts and that the thermal safety margin for both hosts and parasitoids is smaller in environments that experience more extreme temperatures; the authors also infer that host–parasitoid food webs are more unstable than previously thought, with important implications for top down control of herbivores.

62. Parker AL, Kingsolver JG: **The interactive effects of heat stress, parasitism and host plant quality in a host–parasitoid system**. *Funct Ecol* 2024, **38**:642-653.

63. Godfray HCJ: **Parasitoids: Behavioral and Evolutionary Ecology**. Princeton University Press; 2019.

64. Kingsolver JG, Buckley LB: **Ontogenetic variation in thermal sensitivity shapes insect ecological responses to climate change**. *Curr Opin Insect Sci* 2020, **41**:17-24.

65. Ismaeil I, Doury G, Desouhant E, Dubois F, Prevost G, Couty A: **Trans-generational effects of mild heat stress on the life history traits of an aphid parasitoid**. *PLoS One* 2013, **8**:e54306.

66. Dumser JB: **The regulation of spermatogenesis in insects**. *Annu Rev Entomol* 1980, **25**:341-369.

67. Bahar MH, Hegedus D, Soroka J, Coutu C, Bekkaoui D, Dosdall L: **Survival and Hsp70 gene expression in *Plutella xylostella* and its larval parasitoid diadegma insulare varied between slowly ramping and abrupt extreme temperature regimes**. *PLoS One* 2013, **8**:e73901.

68. • Forlano P, Caccavo V, Battaglia D, Fanti P, Trotta V: **Effects of exposures to repeated heat stress on the survival of the pea aphid *Acyrthosiphon pisum* and its endoparasitoid *Aphidius ervi***. *Bull Insect* 2023, **76**:219-227.

An empirical study that demonstrates thermal mismatch in heat-hardening capacity between an aphid parasitoid and its host and a surprising improval of parasitized host short-term survival to heat stress possibly due to shared physiological stress mechanisms.

69. Beckage NE, Gelman DB: **Wasp parasitoid disruption of host development: implications for new biologically based strategies for insect control**. *Annu Rev Entomol* 2004, **49**:299-330.

70. Adamo SA, Kovalko I, Turnbull KF, Easy RH, Miles CI: **The parasitic wasp *Cotesia congregata* uses multiple mechanisms to control host (*Manduca sexta*) behaviour**. *J Exp Biol* 2016, **219**:3750-3758.

71. Drezen J-M, Chevignon G, Louis F, Huguet E: **Origin and evolution of symbiotic viruses associated with parasitoid wasps**. *Curr Opin Insect Sci* 2014, **6**:35-43.

72. Burke GR, Strand MR: **Systematic analysis of a wasp parasitism arsenal**. *Mol Ecol* 2014, **23**:890-901.

73. Cuny MAC, Poelman EH: **Evolution of koinobiont parasitoid host regulation and consequences for indirect plant defence**. *Evol Ecol* 2022, **36**:299-319.

74. Strand MR: **Teratocytes and their functions in parasitoids**. *Curr Opin Insect Sci* 2014, **6**:68-73.

75. Tougeron K, Brodeur J, Le Lann C, van Baaren J: **How climate change affects the seasonal ecology of insect parasitoids**. *Ecol Entomol* 2020, **45**:167-181.

76. Pincebourde S, Woods HA: **Climate uncertainty on leaf surfaces: the biophysics of leaf microclimates and their consequences for leaf-dwelling organisms**. *Funct Ecol* 2012, **26**:844-853.

77. Woods HA, Legault G, Kingsolver JG, Pincebourde S, Shah AA, Larkin BG: **Climate-driven thermal opportunities and risks for leaf miners in aspen canopies**. *Ecol Monogr* 2022, **92**:e1544.

78. Lemoine MM, Engl T, Kaltenpoth M: **Microbial symbionts expanding or constraining abiotic niche space in insects**. *Curr Opin Insect Sci* 2020, **39**:14-20.

79. Skendžić S, Zovko M, Pajač Živković I, Lešić V, Lemić D: **Effect of climate change on introduced and native agricultural invasive insect pests in Europe**. *Insects* 2021, **12**:985.