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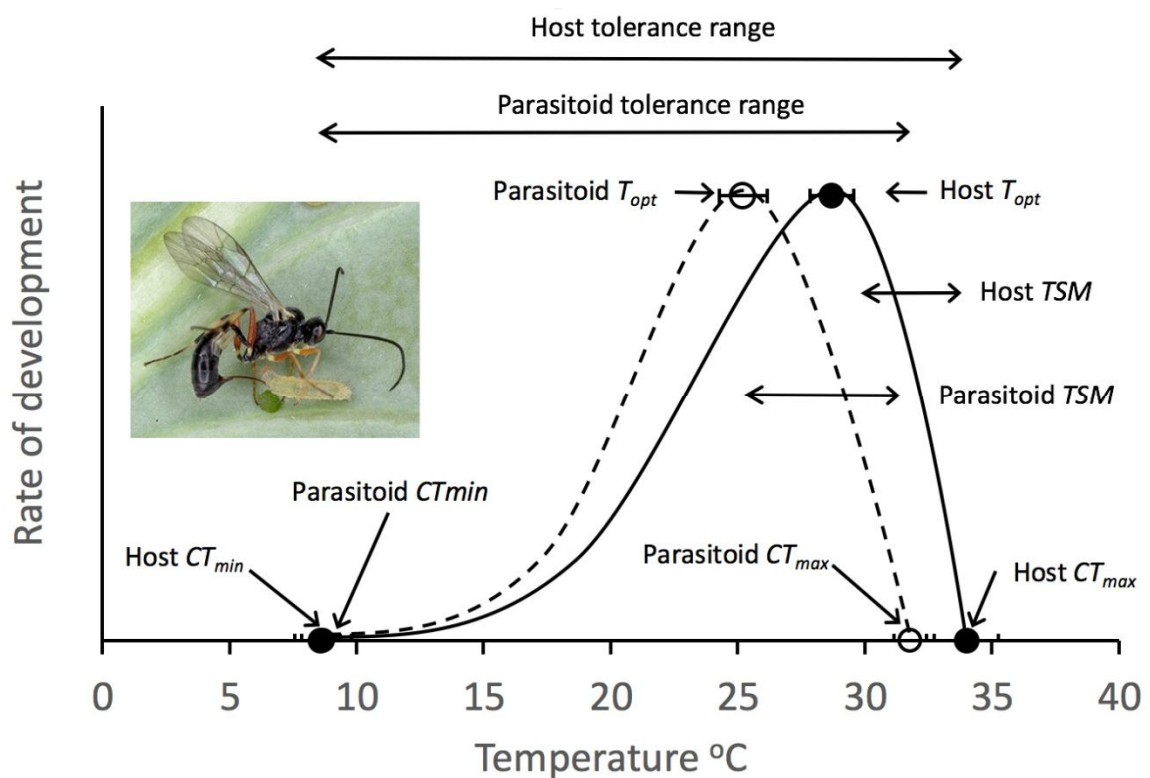
Climate change and biological control: the consequences of increasing temperatures on host-parasitoid interactions

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Graphical abstract



Highlights

- Evidence for fundamental differences in the responses of parasitoids and their hosts to temperature
- In the context of increasing global temperatures differences will favor hosts over parasitoids
- Predicted climate change could exclude parasitoids from locations where they currently persist
- Further research on effects of increasing temperatures on a wider range of fitness traits required

Abstract

The relative thermal requirements and tolerances of hymenopteran parasitoids and their hosts were investigated based on published data. The optimal temperature (T_{opt}) for development of parasitoids was significantly lower than that for their hosts. Given the limited plasticity of insect responses to high temperatures and the proximity of T_{opt} to critical thermal maxima, this suggests that host-parasitoid interactions could be negatively affected by increasing global temperatures. A modelling study of the interactions between the diamondback moth and its parasitoid *Diadegma semiclausum* in Australia indicated that predicted temperature increases will have a greater negative impact on the distribution of the parasitoid than on its host and that they could lead to its exclusion from some agricultural regions where it is currently important.

Introduction

Elevated concentrations of greenhouse gases in the atmosphere are leading to measurable increases in temperatures at the Earth's surface. This is likely to result in more extreme variation in local temperatures and increased frequencies and durations of heatwaves, periods of drought and extreme precipitation events. Climate change imperils global food security by compromising agricultural production, contributing to elevated food prices and increasing the risks of hunger and malnutrition [1]. Together, current agricultural practices and the conversion of land for agricultural production are responsible for approximately 30% of greenhouse gas emissions [2], exacerbating the problems that climate change poses to agriculture and leading to calls for a clear foundation for the sustainable intensification of agricultural practices [2,3]. The prevailing effects of climate change have already caused organismal range shifts and population changes, and they are increasingly considered to pose a risk to species extinctions [4].

The biological control of pests of food crops is a key ecosystem service that underpins sustainable approaches to their management, thereby providing significant fiscal and environmental benefits [5]. Classical biological control, the introduction of a natural enemy of an injurious organism from its region of origin into the region invaded by the pest, has its modern foundation in the establishment of *Rodolia cardinalis* and *Cryptochaetum iceryae* in Californian citrus groves to control the invasive scale insect, *Icerya purchasi*. Since then many successful classical biological control programs have been implemented [5], notably the control of cassava mealybug (*Phenacoccus manihoti*) in sub-Saharan Africa by introduction of the encyrtid parasitoid *Epidinocarsis lopezi* [6] and management of the diamondback moth (*Plutella xylostella*) in many locations by introduction of one or more members of a parasitoid complex [7]. The impacts of climate change on host-parasitoid interactions, whether natural enemies have been deliberately introduced into new regions or whether the agents are indigenous and biological control is being supported by conservation practices, will be modulated by direct effects on the organisms involved (e.g. through effects on physiology and metabolism), the responses of those organisms and subsequent tri-trophic interactions. Parasitoids, which represent the third trophic level, are likely to be significantly affected by climate induced perturbations to these systems and understanding what these effects might be is of critical importance.

Thermal biology and host-parasitoid interactions

Insects are ectotherms and their body temperatures reflect the temperatures that they experience in their local environment. Insect metabolism, growth, movement and reproduction are temperature-dependent and we can begin to understand the likely impacts of climate change on host-parasitoid interactions by considering how temperature might affect relative fitness. By measuring a surrogate for fitness or “performance” (e.g. development rate), the response of insects across a range of temperatures can be estimated and used to construct Thermal Performance Curves (*TPCs*) [8**]. Typically, such curves increase gradually with temperature from the critical thermal minimum (CT_{min} , lower thermal limit of performance) to a maximum (T_{opt} , temperature at which performance is maximized) and then decline rapidly as the critical thermal maximum (CT_{max} , upper thermal limit of performance) is approached [8**]. Interpretation of *TPCs* and the implications for how organisms might be expected to respond to changes in temperature need to be exercised with care as responses to temperature of a given species typically vary between different ontogenic stages, fitness traits and individuals that have been held at different temperatures prior to the start of studies [8**,9**]. Nevertheless, provided that their constraints are appreciated and if they are constructed from appropriate data, *TPCs* can provide significant insight into the thermal biology of ectotherms and how they might respond to increasing global temperatures.

Much of the research that has investigated the responses of parasitoids to extreme temperatures has focused on lower thermal limits, with more recent studies considering how warmer conditions could lead to the decoupling of phenological synchrony between parasitoids and their hosts based on differences between their lower thermal limits [10*]. Differences between the *TPCs* of parasitoids and their hosts will result in different responses to given temperature conditions, resulting in changed relative development rates that will affect their population biology. If the critical parameters of the *TPC* for a parasitoid are lower (to the left) than those of the corresponding *TPC* for its host then increased temperatures are likely to have a greater impact on the parasitoid than on its host. The upper thermal limits for insects tend to vary much less than the lower thermal limits in response to acclimation or acclimatization, they are restricted to a narrow range that is typically close to T_{opt} and that their evolution appears to be tightly constrained [9**]. Consequently, rising global temperatures are likely to pose significant problems for insects.

In host-parasitoid interactions the relative nature of host and parasitoid *TPCs* will have profound consequences for the outcomes of these relationships.

We searched the published literature for reports of studies that investigated the thermal performance of parasitoids developing in their hosts (Table 1). Studies were selected if they reported the basic metrics of parasitoid *TPCs* (CT_{min} , T_{opt} and CT_{max}) based on development rate and either also reported these metrics for the respective host, or involved a host species for which these metrics had been determined independently (Table 1). In addition to development, 14 of the 17 studies (82%) reported on parasitoid survival to the adult stage, 65% on adult parasitoid longevity, 82% on parasitoid sex ratios. Only 41% of the studies measured parasitoid fecundity and 29% estimates rates of host parasitism (data not shown). When critical values from *TPCs* based on development rates were compared between parasitoids and their hosts, no statistical difference was detected between estimates of the host and parasitoid CT_{min} (mean difference (\pm SE)=0.09 (\pm 1.13); t_{16} =0.078, P =0.938), CT_{max} (mean difference (\pm SE)= 2.18 (\pm 1.09); t_{16} =2.017, P =0.061), tolerance range (difference between CT_{max} and CT_{min}) (mean difference (\pm SE)= 2.10 (\pm 1.22); t_{16} =1.715, P =0.106) or Thermal Safety Margin (*TSM*; difference between T_{opt} and CT_{max}) (mean difference (\pm SE)= 1.3 (\pm 0.72); t_{16} =1.796, P =0.092) (Table 1, Figure 1). However, the estimated T_{opt} for parasitoids was consistently significantly lower than the estimated T_{opt} for their hosts (mean difference (\pm SE) =3.49 (\pm 1.36); t_{16} =2.564, P =0.021) (Table 1, Figure 1). This suggests that in general, parasitoids might be more susceptible to elevated temperatures than their hosts. This is supported by reports of changed behaviors in parasitized hosts that lead to reduced [11] and increased [12] exposure to high temperatures that result in increased and decreased parasitoid survival respectively.

Studies investigating the effects of fluctuating temperatures on parasitoids are rare and none were included in our analysis. In terrestrial environments temperature fluctuates daily and the magnitude of the diurnal oscillations vary between seasons and different habitats. The asymmetrical nature of *TPCs* (Figure 1) mean that changes in temperature will produce different effects, depending on whether or not the variation encompasses T_{opt} . As T_{opt} is typically close to CT_{max} , small increases in temperature can result in this threshold being exceeded; at temperatures below T_{opt} the rate of change is lower (Figure 1) and larger temperature changes can be experienced before critical lower thresholds are crossed

[13**]. Thus, at temperatures below T_{opt} insects developing under fluctuating temperatures will develop more quickly than insects developing under constant temperatures with an equivalent mean; the effect is amplified by greater temperature variation. At temperatures above T_{opt} the opposite occurs and temperature oscillations that result in T_{opt} being exceeded yield diminished development rates during that part of the temperature cycle. Consequently, studies conducted at constant and fluctuating temperatures will have different outcomes and the magnitude of this difference is dependent on the amplitude of the temperature changes. *TPCs* must be constructed using biologically meaningful data if they are to be of use in investigations of the impact of environmental change on organisms [8**]. We used the only readily available data, development rate, as a proxy for fitness to investigate the relative effects of temperature on parasitoids and their hosts. Other fitness traits are likely to be influenced differently and the precise manner in which these might be modulated by different fluctuating temperature regimes is unknown. Further, most of the studies investigated do not report on acclimation of organisms prior to the start of experiments, the optimality of the diets used is unknown and in many of our comparisons studies on hosts and parasitoids were conducted independently. Nevertheless, there is a clear suggestion that T_{opt} for parasitoids is typically lower than T_{opt} for their hosts and this warrants further investigation.

Case study: modelling the effects of climate change on a host- parasitoid interaction

Plutella xylostella is a global pest of *Brassica* crops that has been successfully managed in many regions by classical biological control with the hymenopteran larval-pupal parasitoid, *Diadegma semiclausum* [7]. T_{opt} for the parasitoid is estimated to be significantly lower than that for its host [14*] and integration of host and parasitoid CLIMEX models predict that projected climatic conditions by 2070 are likely lead to reduced biological control of the pest throughout much of its established range [14*]. Consistent with observations, the models predict that current conditions for the parasitoid are least conducive across northern Australia (Figure 2a, dark red regions) but that these improve in southeast Queensland (Figure 2a, Zone A) and improve further still through New South Wales and into Victoria (Figure 2a, Zone B). In southern Victoria, southern South Australia, Tasmania and south west Western Australia the models indicate that current conditions are more suitable for *D. semiclausum* than for its host (Figure 2a, blue regions). By 2070, conditions in large areas of

central Australia are likely to be unsuitable for *P. xylostella* (Figure 2b), however, conditions in south eastern Queensland and northern New South Wales (Figure 2b, Zone A) are predicted to favour the pest over its parasitoid and the projected higher temperatures in these regions could exclude this important biological control agent from regions where it is currently established and where it contributes important ecosystem services to agriculture [15]. Similarly, the suitability of conditions for the parasitoid are predicted to decline through southern regions of New South Wales, eastern Victoria and south western West Australia (Figure 2b, Zones B and C), but effects on the host-parasitoid interaction are likely to be limited in Tasmania (Figure 2b).

Conclusions and future research

TPCs provide a clear and recognized framework for the investigation of the effects of temperature on ectotherms. The analysis presented suggests that there may be general differences between the thermal requirements and tolerances of parasitoids and their hosts (Figure 1). In the context of increasing global temperatures these incongruities could contribute asymmetrical outcomes in host-parasitoid interactions, resulting in reduced parasitoid efficacy and the possible exclusion of parasitoids, but not their hosts, from locations in which they currently co-exist. The data set that was compiled is small, it only investigated one fitness trait (development rate) and it is limited to studies conducted at constant temperatures. Although some studies have investigated aspects of the thermal biology of parasitoids and their hosts simultaneously [29], the vast majority of studies reporting on the thermal requirements of parasitoids do so without reporting on similar studies for their hosts. This creates problems, as comparison of disparate studies introduces significant sources of error (e.g. possible genetic differences between study populations, differences between acclimation conditions, diet or methodological approaches) that can be confounding. Rigorous studies that use a wider range of fitness traits and explicitly seek to investigate the thermal requirements and tolerances of both organisms in specific host-parasitoid interactions are required. This will allow investigation of how temperature manipulations can affect the outcome of these interactions so that predictions of the effects of climate change can be tested with greater precision. In interactions between *P. xylostella* and *D. semiclausum*, CLIMEX models based on developmental responses to temperature in the laboratory and known spatial and temporal distributions of both organisms indicate that

the parasitoid might indeed be more profoundly affected by predicted climate change in areas of Australia where it is currently of agricultural importance. Refining this approach and supporting it with the requisite empirical data, can provide a mechanism for investigating the likely effects of climate change on other specific host-parasitoid interactions, some of which are indispensable to current agriculture.

Acknowledgements

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Figure Captions

Figure 1: Thermal performance curves that relate rearing temperature to development rate (fitness) for parasitoids and their hosts. The curves are diagrammatic but the critical values plotted for host and parasitoid critical thermal minima (CT_{min}), critical thermal maxima (CT_{max}) and optimal temperatures (T_{opt}) represent the mean (\pm SE) values calculated from the data in Table 1, see text for details. Thermal safety margin (TSM) is the difference between T_{opt} and CT_{max} .

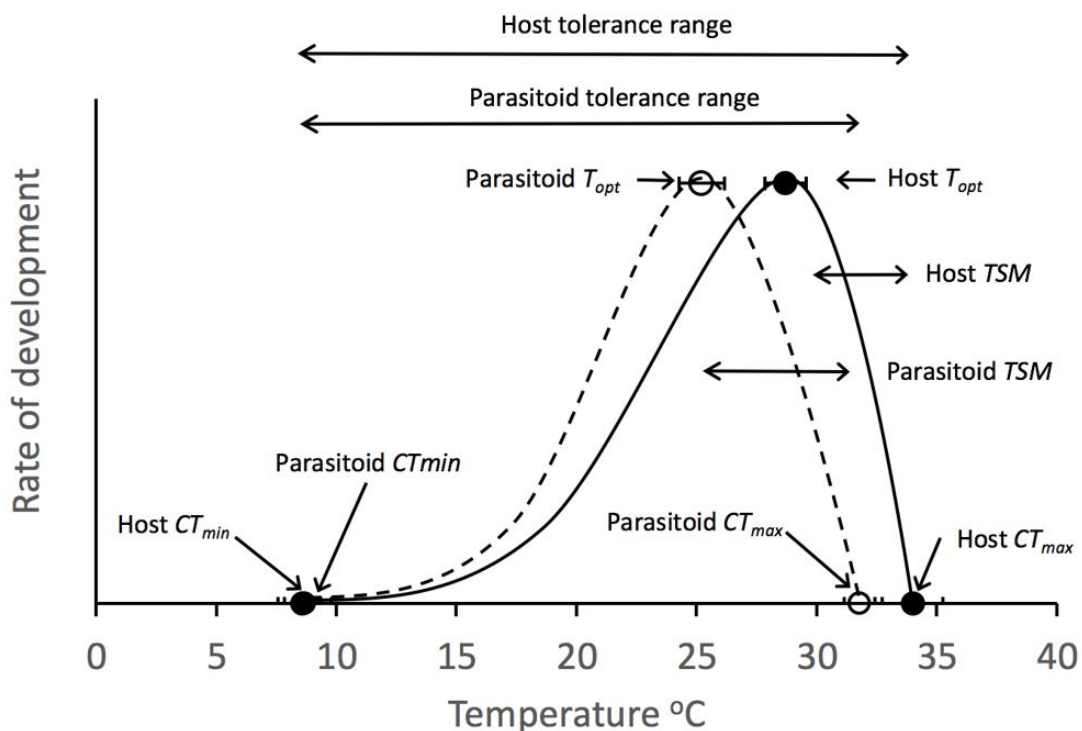
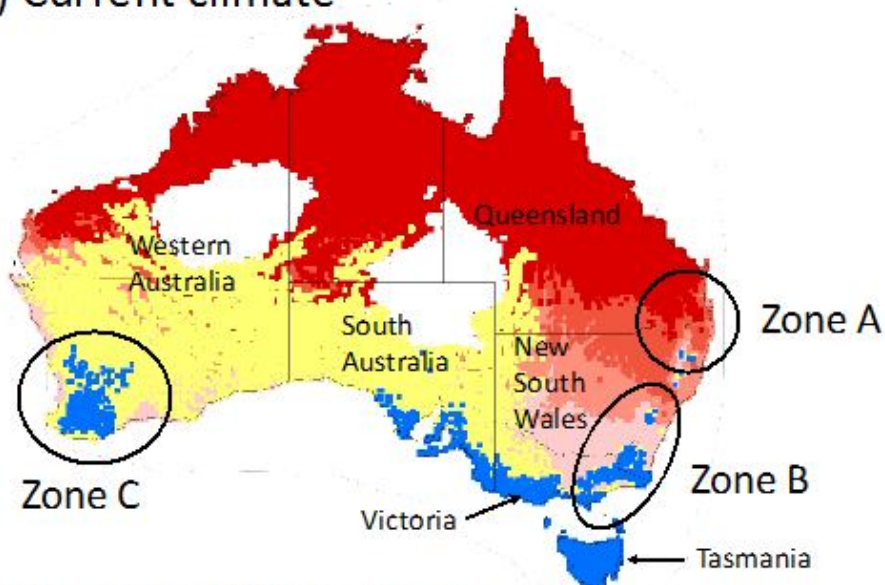


Figure 2. The relative suitability of locations in Australia for *Plutella xylostella* and its parasitoid *Diadegma semiclausum* as predicted by combined CLIMEX models under **a)** current climate and **b)** predicted climate by 2070 [14]. Relative suitability for *P. xylostella* (RS_{Px}) = $[(GI_{Px} - GI_{Ds}) / GI_{Px}]$ where GI_{Px} = annual growth index for *P. xylostella* and GI_{Ds} = annual growth index for *D. semiclausum* [14]. White = locations not suitable for *P. xylostella* ($GI_{Px} = 0$). Yellow = locations where conditions are equally suitable for *P. xylostella* and *D. semiclausum* ($GI_{Px} = GI_{Ds}$). Blue = locations where suitability for *D. semiclausum* is greater than that for *P. xylostella* ($GI_{Ds} > GI_{Px}$). In all other locations (dark red through pink) conditions are more suitable for *P. xylostella* than for *D. semiclausum* ($GI_{Px} > GI_{Ds}$): dark red = locations which favour *P. xylostella* over *D. semiclausum* most ($RS_{Px} > 0.45$); red ($RS_{Px} = 0.31 - 0.45$); light red ($RS_{Px} = 0.16 - 0.30$); pink ($RS_{Px} = 0.01 - 0.15$). By 2070 predicted climate

change is likely to increase the relative suitability of locations in Zone A for *P. xylostella* considerably, almost eliminate the current advantage of *D. semiclausum* over *P. xylostella* in Zone B and significantly reduce that advantage in Zone C.

a) Current climate



b) Predicted 2070 climate

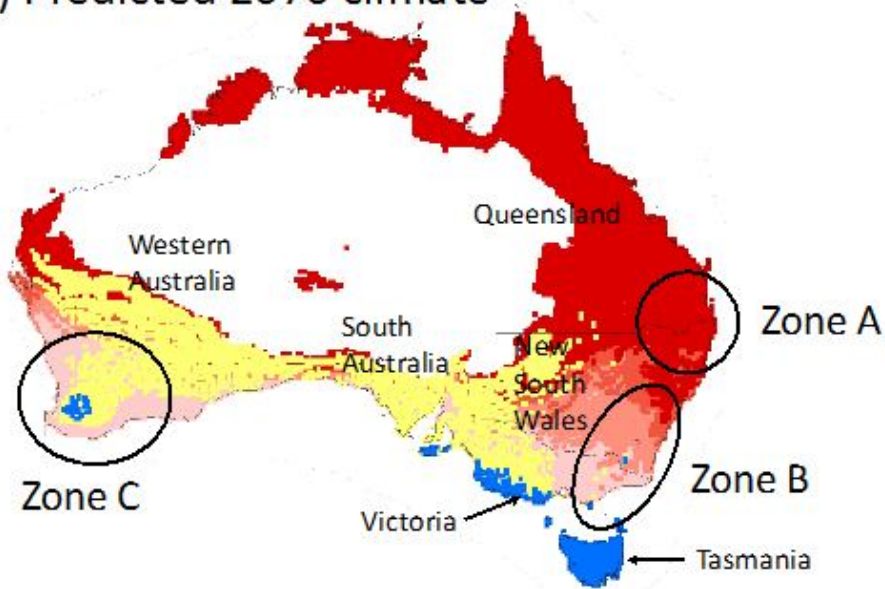


Table 1. Published studies reporting the critical thermal limits of parasitoids and their host insects

Host				Parasitoid						
Species (Order)	CT _{min}	T _{opt}	CT _{max}	Species (all Hymenoptera)	Host stage attacked	Temp			References	
						CT _{min}	T _{opt}	CT _{max}		range (°C)
<i>Heliiothis virescens</i> (Lepidoptera)	13.0	31.5	35.0	<i>Trichogramma acacioi</i>	Egg	9.9	25.0	30.0	20-30	[16], [17]
<i>Diaprepes abbreviatus</i> (Coleoptera)	11.0	26.0	30.0	<i>Fidiobia dominica</i>	Egg	9.6	27.6	30.0	9-36	[18], [19]
<i>Diaprepes abbreviatus</i> (Coleoptera)	11.0	26.0	30.0	<i>Haeckeliana sperata</i>	Egg	11.3	31.0	35.0	9-36	[18], [19]
<i>Diaprepes abbreviatus</i> (Coleoptera)	11.0	26.0	30.0	<i>Aprostocetus vaquitarum</i>	Egg	15.8	30.9	33.0	5-40	[20], [19]
<i>Diaprepes abbreviatus</i> (Coleoptera)	11.0	26.0	30.0	<i>Quadrastichus haitiensis</i>	Egg	16.0	32.0	33.8	5-33	[21], [19]
<i>Ceratitis capitata</i> (Diptera)	10.0	35.6	47.0	<i>Aganaspis daci</i>	Larva	8.5	25.0	35.0	15-35	[22], [23]
<i>Bactrocera invadens</i> (Diptera)	9.7	30.0	35.0	<i>Diachasmimorpha longicaudata</i>	Larva	9.0	20.0	31.0	15-35	[24], [25]
<i>Bactrocera invadens</i> (Diptera)	9.7	30.0	35.0	<i>Fopius arisanus</i>	Larva	8.0	20.0	35.0	15-35	[24], [25]
<i>Thecodiplosis japonensis</i> (Diptera)	5.0	27.0	30.0	<i>Platygaster matsutama</i>	Larva	4.2	24.8	30.0	12-30	[26], [27]
<i>Thecodiplosis japonensis</i> (Diptera)	5.0	27.0	30.0	<i>Inostemma seoulis</i>	Larva	8.4	26.5	30.0	12-30	[26], [27]
<i>Plutella xylostella</i> (Lepidoptera)	7.4	30.0	38.0	<i>Diadegma semiclausum</i>	Larva	6.0	20.0	30.0	10-30	[28], [29]
<i>Spodoptera exigua</i> (Lepidoptera)	13.0	32.0	35.0	<i>Microplitis manilae</i>	Larva	11.0	28.0	33.0	17-32	[30], [31]
<i>Macrosiphum euphorbiae</i> (Hemiptera)	5.0	20.0	27.0	<i>Aphidius ervi</i>	Nymph	12.0	20.0	28.0	12-28	[32], [33]
<i>Apolygus lucorum</i> (Hemiptera)	3.5	32.0	40.0	<i>Peristenus spretus</i>	Nymph	7.3	23.0	33.0	15-35	[34], [35]
<i>Diaphorina citri</i> (Hemiptera)	10.5	30.0	41.0	<i>Tamarixia radiata</i>	Nymph	-3.6	25.0	36.0	15-35	[36], [37]
<i>Sitobion avenae</i> (Homoptera)	4.0	29.0	30.0	<i>Aphidius rhopalosiphii</i>	Nymph	3.5	25.0	27.0	10-25	[38], [39]
<i>Diatraea saccharalis</i> (Lepidoptera)	8.0	30.0	35.0	<i>Trichospilus diatraeae</i>	Pupa	9.4	25.0	31.0	16-31	[40], [41]