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## RESEARCH ARTICLE

# Predicting population dynamics of the parasitoid *Cotesia marginiventris* (Hymenoptera: Braconidae) resulting from novel interactions of temperature and selenium

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Changes in trophic level interactions due to global climate change and the increasing occurrence of pollution are likely to have consequences for natural enemies. Specifically, information regarding the effects of these factors on insect parasitoids is relatively sparse. We examined the individual and joint effects of temperature and the pollutant selenium on the fitness correlates of the parasitoid wasp *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae), parasitizing *Spodoptera exigua* (Hubner) (Lepidoptera: Noctuidae). Our specific objective was to determine in a factorial experiment how three temperatures (constant 28.6°C, constant 33°C and a fluctuating temperature between 28.6 and 33°C) and three concentrations of seleno-DL-methionine (0.00, 21.21, and 42.42 µg/g) affected the parasitoid's fitness and life history. Parasitoids failed to complete development at the constant 33°C, but developed significantly faster at the fluctuating temperature compared to the constant 28.6°C. There were significant declines due to increased temperature, but not selenium, on *C. marginiventris* survival time, adult body weight, body size, hind tibia length, female life span and number of progeny that survived to adulthood. Mean generation times and the intrinsic rate of increase ( $r$ ) further show that both of these life table statistics declined under conditions of increased temperatures. We discuss the implications of these results in helping to understand and predict the effectiveness of biological control programs and pest management strategies as climate changes in the presence of metal and metalloid pollution.

**Keywords:** climate change; pollution; selenium; parasitoids; fitness correlates

## Introduction

Global climate change can affect a species' population abundance, distribution, and life history (Easterling et al. 2000; Bale et al. 2002). Climate change is expected to result in increasing temperatures, extremes in precipitation events, and sea level rise (Karl and Trenberth 2003). Increases in temperature can directly impact an insect's survival, development, growth, and fecundity (Chapman 1975; Sehgal, Das, Chander, Gupta, and Kalra 2006). Insect herbivores often respond rapidly and dramatically to climatic conditions (e.g., temperature and precipitation) which influence development, thereby leading to large temporal variances in populations (Stireman et al. 2005; Trumble and Butler 2009). However, parasitoids and other

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natural enemies may be affected by both unpredictable climatic variation and the unpredictable amplified variance in host dynamics in response to climate (Stireman et al. 2005). Thus, the impacts of climate change are likely to have consequences on higher trophic levels that depend on the capacity of the lower trophic levels to adapt to these changes (Hance, Baaren, Vernon, and Boivin 2007). Parasitoids are expected to face severe ecological repercussions of elevated temperatures from climate change such as an alteration of the synchronization between host and parasitoid caused by a divergence between their thermal preferences, elimination of endosymbionts, and changes in geographic distributions (Coley 1998; Hance et al. 2007). In natural systems, increased temperatures have been reported to cause a decline in the cumulative morphospecies richness of parasitoids (Villalpando, Williams, and Norby 2009). The implications of increased temperatures resulting from global warming are expected to be significant. Quantifying the effects of increasing temperatures on insect parasitoids will aid in using these species successfully in integrated pest management and biological control programs, and determining how ecosystem services of parasitoids will change with global warming.

Another pertinent environmental concern is anthropogenic pollution. Human-induced pollution has also modified insect population structures and ecosystems (Heliövaara and Vaisanen 1993). Pollution-induced environmental changes likewise have effects that can disrupt tritrophic interactions in terrestrial systems (Alstad, Edmunds, and Weinstein 1982; Hughes 1988; Reimer and Whittaker 1989; Fluckiger, Braun, and Hiltbrunner 2002). However, the impacts of pollutants on parasitoids have seldom been studied (Butler, Beckage, and Trumble 2009).

In California's San Joaquin Valley, selenium (Se) emerged in the 1980s as an environmental problem due to the drainage of agricultural wastewater (Burau 1985). Selenium leached from the soil was the source of contamination of the Kesterson Reservoir in central California with negative effects on fish and waterfowl populations (Barceloux 1999). In an effort to alleviate the Se pollution in this area, phytoremediation strategies (i.e., plant-based technology in which plants are selected to accumulate and volatilize toxic substances from the soil or water) were studied (Nyberg 1991; Parker and Paige 1994; Banuelos et al. 1996, 1997; Wu, van Mantgem, and Guo 1996) as well as possible trophic interactions that insects may have with Se-accumulating plants (Banuelos et al. 2002; Vickerman et al. 2002a; Vickerman, Young, and Trumble 2002b; Vickerman and Trumble 2003; Vickerman, Trumble, George, Pickering, and Nichol 2004). Various forms of Se are known to transfer between plants, herbivores and natural enemies (Vickerman and Trumble 2003; Vickerman et al. 2004), with a tendency for biomagnification (Banuelos et al. 2002). Comparatively few studies have examined the relative toxicological responses of higher trophic levels of Se accumulated in prey or hosts (Trumble and Sorensen 2008). Only one study has examined the effects of the pollutant selenium on a parasitoid (Vickerman et al. 2004), but this paper did not consider the effects of increasing temperatures that are known to substantially change many insect physiological processes (Chapman 1975).

Based on the combined environmental concerns California is likely to face in the future with climate change (Diffenbaugh, Giorgi, and Pal 2008; Trumble and Butler 2009) and elevated Se in the Central Valley of California, a key objective of this study was to quantify the independent and joint effects of increased temperatures and Se on fitness correlates of the parasitoid wasp, *Cotesia marginiventris* (Cresson)

(Hymenoptera: Braconidae), using the beet armyworm, *Spodoptera exigua* (Hubner) (Lepidoptera: Noctuidae) as a host. This parasitoid has been used as a model organism for other studies regarding tritrophic interactions between plants, herbivores, and natural enemies, in particular attraction to host plants (Rostas and Wolflings 2009, and references therein), and recent research has also been conducted regarding the use of this species as a biological control agent of lepidopterans in greenhouses (Riddick 2004, and references therein). The range of *S. exigua* broadly overlaps regions of North America where Se contamination occurs (Pogue 2002). *Cotesia marginiventris* is distributed throughout North, Central, and South America and is an important solitary endoparasitoid of *S. exigua* (Riddick 2006). The goal of this research was also to determine the population dynamics of this wasp in the context of climate change and Se pollution as a model system to investigate the effects these factors may have on higher trophic levels. Predicting how environmental concerns such as climate change and pollution might affect tritrophic interactions (particularly for higher trophic levels) and the structure of ecological communities is critical for understanding changes that could occur in the future. A better understanding of the impact of these environmental factors on parasitoid fitness will allow improved predictions and management of possible population-level effects on ecosystem services.

## Materials and methods

### *Insect colonies*

*Cotesia marginiventris* used in this study were laboratory reared from individuals originally obtained from Tifton, GA. The colony was obtained August 2006 and completed an estimated 10 generations before experiments were initiated. The colony was also periodically augmented (at least annually) with locally collected *C. marginiventris* adults to prevent founders effects and maintain genetic variability. Parasitoids were reared on a laboratory bench under ambient conditions of 23°C and 35–40% RH. Adult parasitoids (200–300 per cage, with an estimated 50:50 sex ratio of females to males) were kept in polypropylene cages (27.5 × 27.5 × 27.5 cm) with 10% honey/water solution. The parasitoid colony was maintained by exposing adult *C. marginiventris* to 600 late first instar *S. exigua* larvae reared on meridic diet (Bio-Serv diet, Frenchtown, NJ) for 2 days. Thirty parasitized larvae were each placed in 210 mL food cups (Sweetheart Cup Co. Inc., Chicago, IL) with meridic diet. Once the *C. marginiventris* larvae emerged from the host and pupated, the cocoons were harvested. Host insects were obtained weekly as eggs from Benzon Research Inc. Eggs were glued to the lids of 210 mL food cups with meridic diet. Cups with eggs were then placed in an environmental growth chamber at 26.7°C, 35–40% RH, and a photoperiod of 16 h L:8 h D.

### *Parasitoid life history experiment*

A factorial experiment was initiated to investigate the effects of temperature and seleno-DL-methionine on *C. marginiventris* fitness correlates. The temperatures were: constant 28.6°C, constant 33°C, and fluctuating temperatures between 28.6 (14 h/day) and 33°C (10 h/day). The 28.6°C represents the average temperature in

Riverside, CA during the month of July (<http://www.weather.com>). The constant 33°C temperature represents a 4.4°C increase in the average temperature to simulate climate change as predicted in the upcoming decades (IPCC 2007); yet this is a temperature in which the host *S. exigua* can develop normally at the constant temperatures of at least 35°C, and some larvae will survive even at 38°C (Ali and Gaylor 1992). The fluctuating temperature provides an added level of realism due to fluctuations of temperature throughout a day. Diets were prepared to provide equal to or greater than 50% mortality based on the lethal concentration (LC<sub>50</sub>) values of seleno-DL-methionine (as much of the Se in non-accumulating species of plants is found as protein-bound selenomethionine, Mayland 1994) as determined for *S. exigua* from Trumble, Kund, and White (1998). Artificial diets were prepared that contained one of the three levels of seleno-DL-methionine: 0.00 (control), 21.21 (level 1) and 42.42 (level 2) µg/g. Concentrations used in the artificial diets are within environmentally relevant ranges of plants occurring at contaminated sites (Mikkelsen, Page, and Bingham 1989; Wu 1994; Dhillon and Dhillon 2003). Diets were prepared following published protocols of Trumble et al. (1998). The water-soluble form of seleno-DL-methionine was obtained from Sigma Chemical Company (St. Louis, MO, USA). The desired concentrations of seleno-DL-methionine used in experiments were achieved by adding the material to 1500 g diet, blended for 5 min and then dispensed into either 210-mL cups or 30-mL clear plastic cups (Waddington North America Inc., Chelmsford, MA) (ca. 10 mL diet/cup). All experiments were conducted in environmental growth chambers at one of the temperatures listed with 14 h L:10 h D.

To conduct an experiment, late first instar *S. exigua* larvae were randomly chosen and placed in a 210-mL cup with a newly emerged and mated *C. marginiventris* female for parasitization of larvae for 24 h at one of the three temperature treatments and on one of the three seleno-DL-methionine diet concentrations. Blocks 1–5 consisted of 20 host larvae for each of the nine treatments: three temperatures × three selenium concentrations. Blocks 6 and 7 consisted of 30 host larvae for each of the six treatments: two temperatures (28.6°C and the fluctuating temperature) × three selenium concentrations. No parasitoids successfully completed development at the 33°C temperature in Blocks 1–5, which is why for Blocks 6 and 7 this temperature was excluded. After 24 h, the hosts were separated into individual 30-mL cups (one caterpillar/cup) on the same seleno-DL-methionine diet concentrations and placed in an environmental chamber. Parasitized hosts were checked daily until mortality or parasitoid emergence. The parasitoid typically emerged after the fourth instar of *S. exigua*. For each treatment, parasitoid survival and developmental times (number of days for emergence from host and adult eclosion) were determined. Encapsulation rates of *S. exigua* to *C. marginiventris* larvae were also recorded by dissecting ( $N = 147$ ) all remaining fourth instar *S. exigua* larvae that survived past the average emergence time of the parasitoid, and finding evidence of melanized immature stages.

Upon adult parasitoid eclosion, up to five male and five female *C. marginiventris* were randomly chosen from each treatment to measure adult weights, body lengths and hind tibia lengths. Weights were determined on individual adults in the laboratory on a Sartorius 1712 MP8 analytical balance (Sartorius GMBH, Gottingen, Germany) with a precision of  $\pm 0.00001$  g. The rest of the females that emerged were paired with newly emerged males from the colony and placed within a

150-mL plastic cup with 20 host larvae per day to obtain measures of female life span and fecundity (number of eggs oviposited was estimated by counting the number of *C. marginiventris* larvae that emerged from hosts and dissections from dead hosts for the presence of parasitoid larvae). Adults were tested under the same temperature  $\times$  selenium treatments in which they were reared. The  $F_1$  progeny were checked daily until mortality or adulthood.

### ***Selenium analysis***

Artificial diets, host larvae, parasitoid larvae, cocoons, and adults were collected for individual selenium analysis. The number of individuals analyzed are in Table 1. Host larvae and parasitoid larvae were collected the day of parasitoid emergence but before parasitoid pupation. Empty parasitoid cocoons and adults were collected on the day of adult parasitoid eclosion. All samples from all treatment groups were frozen at ( $-60^\circ\text{C}$ ) and subsequently freeze dried. Samples were analyzed for total Se by first using acid digestion with  $\text{HNO}_3/\text{H}_2\text{O}_2$  in a CEM microwave (CEM Corporation, Matthews, NC, USA) and then quantified using Inductively Coupled Plasma-Mass Spectrometry (ICP-MS), which was accomplished by TestAmerica, Inc. (Irvine, CA, USA) using the published protocol of U.S. EPA Method 200.8 (U.S. EPA 1999). Concentrations of selenium of an additional 30 samples were also verified as a double-check using the same protocols (ICP-MS, U.S. EPA Method 200.8) by E. S. Babcock and Sons, Inc. (Riverside, CA, USA), which agreed with the TestAmerica, Inc. results. The E. S. Babcock sample results were not included in the statistical analysis.

### ***Statistical analysis***

The experiment was conducted as a randomized complete block design with seven blocks in time. A nonparametric Kruskal–Wallis Test (PROC NPAR1WAY; SAS Institute 2007) was used to test the differences in total selenium in the various samples (diet, host larvae, *C. marginiventris* larvae, cocoons, and adults) because these data were not normally distributed and showed non-constant variance. These data were also pooled across blocks and temperatures. *Post hoc* separations used the Mann–Whitney *U*-test with a Bonferroni adjustment ( $\alpha = 0.01$ ). For each of the parasitoid life history variables, the main factors of temperature and selenium were analyzed as well as the interactions of temperature and selenium. Proportion parasitism data were only analyzed for Blocks 1–5. Prior to analysis of variance (ANOVA) in a general linear model procedure of SAS version 9.2 (PROC GLM; SAS Institute 2007), data were normalized through an arcsine transformation. Encapsulation rates were analyzed using logistic regression to model the probability of encapsulation of *C. marginiventris* larvae by *S. exigua* in SAS (PROC LOGISTIC; SAS Institute 2007). When a treatment factor was significant ( $P < 0.05$ ), a least significant-difference (LSD) test was used to discriminate differences among the treatment means.

Data on the average amount of time larval *C. marginiventris* survived was analyzed using ANOVA in a weighted general linear model procedure of SAS (PROC GLM; SAS Institute 2007). Survival time data were logit transformed and weighted by sample size (i.e., number of larvae in a treatment). Survivorship curves

Table 1. Mean total selenium concentrations (Se  $\mu\text{g/g}$  dry weight) in samples  $\pm$ SE ( $N$ ) and ranges [Min.–Max.] of total selenium concentrations pooled across blocks and temperatures.

	Control (0.00 $\mu\text{g/g}$ seleno-DL-methionine)	Level 1 (21.21 $\mu\text{g/g}$ seleno-DL-methionine)	Level 2 (42.42 $\mu\text{g/g}$ seleno-DL-methionine)
Artificial diets <sup>1</sup>	0.42 $\pm$ 0.42 a (26) [0.00–10.03]	22.57 $\pm$ 0.34 b (24) [19.47–26.05]	44.48 $\pm$ 0.59 c (28) [22.07–50.56]
<i>Spodoptera exigua</i> larvae	0.08 $\pm$ 0.08 a (33) [0.00–2.64]	23.91 $\pm$ 6.27 b (30) [0.00–105.00]	73.39 $\pm$ 9.04 c (38) [0.00–209.40]
<i>C. marginiventris</i> larvae	0.00 a (6) [0.00–0.00]	68.64 $\pm$ 15.64 b (6) [0.00–114.58]	115.28 $\pm$ 5.26 c (9) [87.08–137.93]
<i>C. marginiventris</i> cocoons	0.00 a (30) [0.00–0.00]	0.00 a (26) [0.00–0.00]	23.44 $\pm$ 8.89 b (27) [0.00–151.96]
<i>C. marginiventris</i> adults	0.00 a (29) [0.00–0.00]	20.62 $\pm$ 11.63 a (24) [0.00–205.88]	115.78 $\pm$ 23.59 b (26) [0.00–381.58]

<sup>1</sup>Means within a row followed by different letters are significantly different.

were also constructed and survivorship of *C. marginiventris* larvae to adulthood was compared among temperature treatments using non-parametric survival analysis with the Sidak multiple comparison adjustment to perform temperature comparisons (PROC LIFETEST; SAS Institute 2007). Larval development rates, total development times, adult body weights and lengths were also analyzed using ANOVA in a weighted general linear model procedure of SAS (PROC GLM; SAS Institute 2007). Data were weighted by the sample size of individuals that successfully emerged from hosts or survived to adulthood. When a treatment factor was significant ( $P < 0.05$ ), a Scheffe test was used to discriminate difference among treatment means.

For the variables hind tibia length, adult female life span, fecundity, and number of progeny that survived to adulthood, data were analyzed with a mixed ANOVA model with blocking, temperature, and selenium as fixed effects and the constructed variable 'environment' (combination of block [time], temperature [chamber], and selenium [diet] treatments) as a random effect in SAS (PROC MIXED; SAS Institute 2007). The variable adult female lifespan was square root transformed, and the variable number of progeny that survive to adulthood was log transformed to homogenize variances. When a treatment factor was significant ( $P < 0.05$ ), a Scheffe test was used to discriminate difference among treatment means.

A life table was also constructed to predict the impact of temperature and selenium on the intrinsic rate of increase ( $r$ ), net reproductive rate ( $R_0$ ), and mean generation time ( $T$ ) for parasitoids. Life table data were not analyzed statistically and were calculated only for treatments in which parasitoid survived to adulthood and reproduced. The intrinsic rate of increase was calculated for treatments by dividing the natural logarithm of  $R_0$  by  $T$  (Ricklefs 1973).  $T$  was calculated as the times spent as an egg, plus time spent as a juvenile and the average weighted age at reproduction (Ricklefs 1973). Times spent as a juvenile and weighted age of reproduction were calculated for each treatment.

## Results

### *Amounts of total selenium in samples*

There were significant differences in the mean total selenium concentrations for each of the samples analyzed (Diet:  $X^2 = 68.50$ ,  $df = 2$ ,  $P \leq 0.0001$ ; *S. exigua* larvae:  $X^2 = 37.93$ ,  $df = 2$ ,  $P \leq 0.0001$ ; *C. marginiventris* larvae:  $X^2 = 15.70$ ,  $df = 2$ ,  $P = 0.0004$ ; *C. marginiventris* cocoons:  $X^2 = 13.23$ ,  $df = 2$ ,  $P = 0.0013$ ; *C. marginiventris* adults:  $X^2 = 37.88$ ,  $df = 2$ ,  $P \leq 0.0001$ ). Mean total selenium concentration and ranges (minimum to maximum) of concentrations are shown in Table 1. For artificial diets, the mean total selenium concentrations increased significantly for each of the selenium treatments (Table 1). Mean total selenium concentrations also were significantly increased for each of the selenium treatments for *S. exigua* and *C. marginiventris* larvae (Table 1). For *C. marginiventris* cocoons and adult samples, the two lower levels of selenium concentrations did not differ significantly in mean total selenium concentrations; however, mean total selenium concentrations were significantly increased at the highest selenium level provided (Table 1). Furthermore, there appeared to be a large range of total selenium concentrations in samples (Table 1). In addition, there were cases in which samples did not contain selenium: *S. exigua*

larvae (control: 32 out of 33 samples, 96.97%; Level 1: 19 out of 30 samples, 63.33%; Level 2: 12 out of 38 samples, 31.58%), *C. marginiventris* larvae (control: 6 out of 6 samples, 100.00%; Level 1: 1 out of 6 samples, 16.67%; Level 2: 0 out of 9 samples, 0.00%), cocoons (control: 30 out of 30 samples, 100.00%; Level 1: 26 out of 26 samples, 100.00%; Level 2: 21 out of 27 samples, 77.78%), and adults (control: 29 out of 29 samples, 100.00%; Level 1: 21 out of 24 samples, 87.50%; Level 2: 8 out of 26 samples, 30.77%).

### Proportion parasitized

There were significant differences in the proportion of *S. exigua* larvae parasitized by *C. marginiventris* adult females based on temperature ( $F=16.66$ ,  $df=2, 42$ ,  $P \leq 0.0001$ , Figure 1). The proportion of larvae parasitized significantly decreased in the constant 33°C (30.6%) as compared to the proportion of larvae parasitized in the constant 28.6°C (71.0%) and the fluctuating temperature (76.7%) treatments. The proportion parasitized in the constant 28.6°C and the fluctuating temperature were not significantly different from each other. There were no significant effects of selenium ( $F=0.23$ ,  $df=2, 42$ ,  $P=0.7980$ ), and the interaction of temperature and selenium was also not significant ( $F=1.80$ ,  $df=4, 42$ ,  $P=0.1467$ ).

### Larval survival and development

*Cotesia marginiventris* survival times were significantly different based on temperature ( $F=40.83$ ,  $df=2, 37$ ,  $P \leq 0.0001$ ). There were no significant effects of selenium ( $F=0.01$ ,  $df=2, 37$ ,  $P=0.9864$ ) and the interaction of temperature and selenium was not significant ( $F=0.32$ ,  $df=4, 37$ ,  $P=0.8597$ ). Parasitoid larvae survival times were significantly different for each of the three temperature treatments (Figure 2). Parasitoid larvae survived on average  $11.11 \pm 0.11$  days (mean  $\pm$  SE) ( $N=334$ ),  $10.57 \pm 0.27$  days ( $N=84$ ), and  $7.50 \pm 0.12$  days ( $N=354$ ) after oviposition at the constant 28.6°C, constant 33.0°C and fluctuating temperatures, respectively.

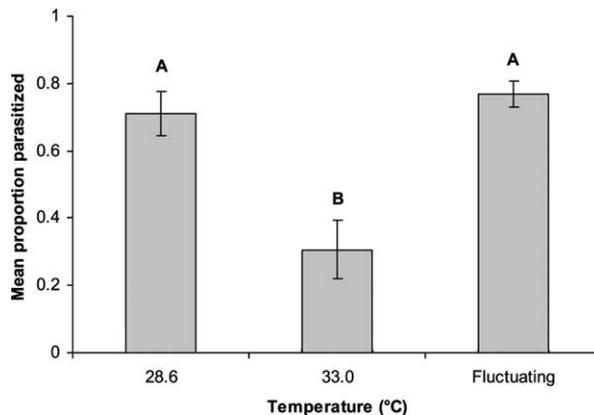


Figure 1. Effect of temperature on the mean proportion (mean  $\pm$  SE) of *Spodoptera exigua* parasitized by *Cotesia marginiventris*.

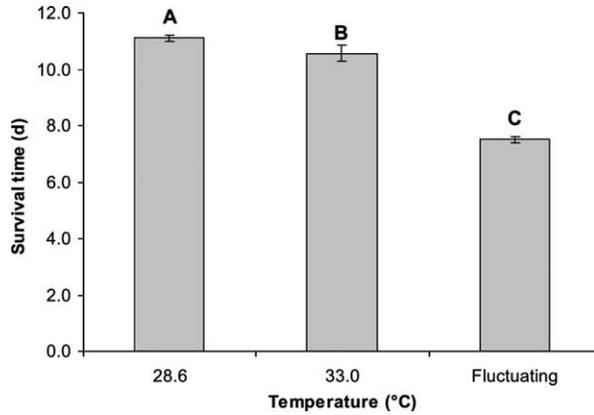


Figure 2. Effect of temperature on average survival time (mean ± SE) of *Cotesia marginiventris* larvae.

Based on this result, survivorship curves of *C. marginiventris* for each of the temperature treatments are shown in Figure 3. Survivorship was significantly affected by temperature ( $X^2 = 388.10$ ,  $df = 2$ ,  $P \leq 0.0001$ ). Survival of *C. marginiventris* larvae reared at the 28.6 and 33°C were not significantly different from each other, but both were significantly greater than the fluctuating temperature, Figure 3. Parasitoids in the constant 28.6 and 33.0°C temperatures exhibited similar patterns of survival with 50% of the individuals alive until ca. days 12 and 11, respectively. Parasitoids in the fluctuating temperatures exhibited decreased survival which declined sharply after day 5 and with 50% of the individuals remaining alive until ca. day 7.

*Cotesia marginiventris* larvae reared at the constant 33°C failed to complete development and died before emergence from the host, thus these data were only analyzed from individuals that successfully emerged from *S. exigua*. There were significant differences in the average time *C. marginiventris* larvae emerged from their hosts' based on temperature ( $F = 84.98$ ,  $df = 1, 36$ ,  $P \leq 0.0001$ ). There were no significant effects of selenium ( $F = 3.24$ ,  $df = 2, 36$ ,  $P = 0.0560$ ), and the interaction

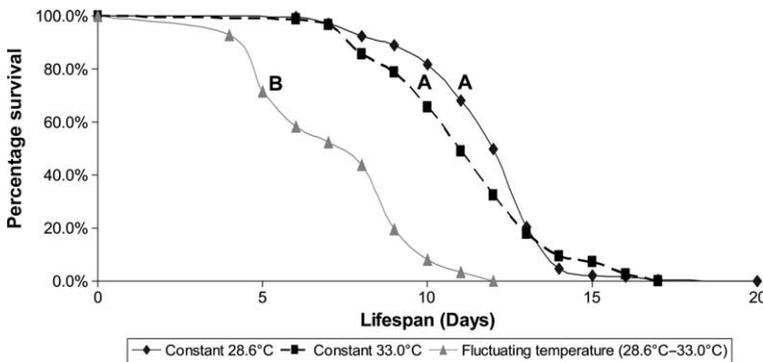


Figure 3. Survivorship curves of larval *Cotesia marginiventris* at three temperatures: constant 28.6°C, constant 33.0°C, and fluctuating temperatures between 28.6 and 33.0°C.

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of temperature and selenium was likewise not significant ( $F=0.74$ ,  $df=2$ ,  $36$ ,  $P=0.4888$ ). Larvae emerged on average from *S. exigua*  $6.92 \pm 0.16$  days ( $N=122$ ) after oviposition at the constant  $28.6^\circ\text{C}$  while parasitoids reared at the fluctuating temperature emerged significantly faster on average from *S. exigua* at  $5.22 \pm 0.12$  days ( $N=110$ ).

For total development time (average time from egg oviposition to adult eclosion), there were significant differences based on temperature ( $F=81.62$ ,  $df=1$ ,  $36$ ,  $P \leq 0.0001$ ). There were no significant effects of selenium ( $F=2.43$ ,  $df=2$ ,  $36$ ,  $P=0.1086$ ) nor was the interaction of temperature and selenium significant ( $F=1.97$ ,  $df=2$ ,  $36$ ,  $P=0.1603$ ). *C. marginiventris* reared at the fluctuating temperatures ( $9.23 \pm 0.21$  days) ( $N=110$ ) emerged as adult significantly faster than parasitoids reared at the constant  $28.6^\circ\text{C}$  ( $11.40 \pm 0.16$  days) ( $N=122$ ).

### **Encapsulation rates**

There were no significant effects of temperature ( $X^2=2.77$ ,  $df=2$ ,  $14$ ,  $P=0.2502$ ), selenium ( $X^2=2.14$ ,  $df=2$ ,  $14$ ,  $P=0.3433$ ), or their interaction ( $X^2=5.00$ ,  $df=4$ ,  $14$ ,  $P=0.2870$ ) on the encapsulation rate of *S. exigua* to *C. marginiventris* immature stages. The encapsulation rate of *S. exigua* larvae to *C. marginiventris* ranged from 0.5 to 32.8% for all the treatments.

### **Adult body weights, body lengths, and hind tibia lengths**

There were significant effects of temperature on the weight of parasitoids ( $F=8.40$ ,  $df=1$ ,  $25$ ,  $P=0.0077$ ). There were no significant effects of selenium ( $F=0.63$ ,  $df=2$ ,  $25$ ,  $P=0.5383$ ) and the interaction term of temperature and selenium was also not significant ( $F=1.45$ ,  $df=2$ ,  $25$ ,  $P=0.2546$ ). Parasitoids reared at the temperature of  $28.6^\circ\text{C}$  weighed ( $980 \pm 50$   $\mu\text{g}$ ) ( $N=133$ ) significantly more than parasitoids in the fluctuating temperatures ( $840 \pm 30$   $\mu\text{g}$ ) ( $N=112$ ).

There were significant effects of temperature on the total body length of parasitoids ( $F=7.42$ ,  $df=2$ ,  $25$ ,  $P=0.0116$ ). There were no significant effects of selenium ( $F=2.04$ ,  $df=2$ ,  $25$ ,  $P=0.1511$ ) and the interaction term of temperature and selenium was not significant as well ( $F=0.80$ ,  $df=2$ ,  $25$ ,  $P=0.4586$ ). Parasitoids exposed to a constant  $28.6^\circ\text{C}$  were significantly longer in total body length ( $2.70 \pm 0.02$  mm) ( $N=122$ ) than parasitoids exposed to the fluctuating temperatures ( $2.62 \pm 0.02$  mm) ( $N=109$ ).

There were significant effects of temperature on *C. marginiventris* hind tibia lengths ( $F=11.04$ ,  $df=1$ ,  $21$ ,  $P=0.0032$ ). There were no significant effect of selenium ( $F=0.62$ ,  $df=2$ ,  $21$ ,  $P=0.5496$ ) and the interaction of temperature and selenium was not significant ( $F=0.16$ ,  $df=2$ ,  $21$ ,  $P=0.8537$ ). Parasitoids reared at a constant  $28.6^\circ\text{C}$  exhibited significantly longer hind tibia ( $0.76 \pm 0.004$  mm) ( $N=122$ ) than parasitoids reared in the fluctuating temperatures ( $0.74 \pm 0.004$  mm) ( $N=109$ ).

### **Female lifespan and fecundity**

Temperature had significant effects on female life span ( $F=11.60$ ,  $df=1$ ,  $5$ ,  $P=0.0158$ ). However, selenium did not exert significant effects on female life span ( $F=1.97$ ,  $df=2$ ,  $5$ ,  $P=0.2243$ ) nor was the interaction of temperature and selenium

significant ( $F=1.52$ ,  $df=2, 5$ ,  $P=0.3034$ ). Females exposed to fluctuating temperatures exhibited significant decreases in lifespan ( $4.10 \pm 0.64$  days) ( $N=10$ ) compared to females in the constant  $28.6^\circ\text{C}$  temperature ( $7.98 \pm 0.46$  days) ( $N=43$ ). Temperature ( $F=7.67$ ,  $df=1, 2$ ,  $P=0.1070$ ), selenium ( $F=0.06$ ,  $df=2, 2$ ,  $P=0.9470$ ), and the interaction of temperature and selenium ( $F=1.27$ ,  $df=1, 2$ ,  $P=0.3604$ ) had no significant effects on the number of eggs *C. marginiventris* females oviposited into *S. exigua* larvae.

Temperature had a significant effect on the number of progeny that survived to adulthood ( $F=34.11$ ,  $df=1, 31$ ,  $P \leq 0.0001$ ). There were no significant effects of selenium ( $F=0.36$ ,  $df=2, 31$ ,  $P=0.7023$ ) and the interaction of temperature and selenium was not significant as well ( $F=0.15$ ,  $df=1, 31$ ,  $P=0.7006$ ). The numbers of progeny that survived to adulthood when reared at the fluctuating temperature were significantly decreased ( $2.8 \pm 0.48$ ) ( $N=4$  females) than progeny reared at the constant  $28.6^\circ\text{C}$  temperature ( $27.6 \pm 2.40$ ) ( $N=37$  females).

### Life table

As a general trend, the net reproductive rate ( $R_0$ ), mean generation times ( $T$ ), and intrinsic rates of increase ( $r$ ) decreased when parasitoids were exposed to fluctuating temperatures when compared to parasitoids exposed to the constant  $28.6^\circ\text{C}$  temperature (Table 2).

### Discussion

Temperature had a substantial influence on *C. marginiventris* development, survival, size, weight, and adult life span. Larval development times decreased with fluctuating temperatures. Developmental times often decline for *C. marginiventris* as temperatures increase (Kunnalaca and Mueller 1979; Rajapakse, Waddill, and Ashley 1992). The constant  $33^\circ\text{C}$  appeared to be lethal to *C. marginiventris* larvae as none completed development at this temperature, although parasitoid larvae were able to survive for an average of 10 days suggesting some development may have taken place in the host. Increasing temperature decreased survival of *C. marginiventris* and reduced the number of progeny that survived to adulthood from parents reared under the higher temperature regimes. Temperature also

Table 2. Net reproductive rate, generation time, and intrinsic rate of increase ( $r$ ) of *Cotesia marginiventris* females exposed to different temperature and selenium levels.

Treatment <sup>1</sup>	Net reproductive rate = $\Sigma l_x m_x$ ( $R_0$ )	Mean generation time ( $T$ , days)	Intrinsic rate of increase ( $r$ )
Constant $28.6^\circ\text{C}$ , 0.00 $\mu\text{g/g}$ Se	37.33	13.23	0.274
Constant $28.6^\circ\text{C}$ , 21.21 $\mu\text{g/g}$ Se	24.33	13.44	0.237
Constant $28.6^\circ\text{C}$ , 42.42 $\mu\text{g/g}$ Se	23.88	14.28	0.222
Fluctuating, 0.00 $\mu\text{g/g}$ Se	3.00	10.59	0.104
Fluctuating, 42.42 $\mu\text{g/g}$ Se	2.75	10.55	0.096

<sup>1</sup>Life table data were not generated for *C. marginiventris* females exposed to fluctuating temperatures at the 21.21  $\mu\text{g/g}$  Se because no  $F_1$  progeny were produced in this treatment.

reduced the total body length, body weights, and hind tibia lengths of *C. marginiventris*, which in other parasitoid species are correlated with fitness (Kazmer and Luck 1995). At least with this study, larger females did not produce more progeny. However, this may be explained, in part, because the eggs were not dissected out of the ovaries and we assumed numbers of eggs were related to the number of larvae that emerged from hosts. This assumption may not have been correct. A study by Riddick (2006) did find a positive relationship between the number of dissected eggs of *C. marginiventris* and hind tibia length; however, this relationship was relatively weak due to a large amount of variability. Further, temperature significantly decreased the proportion of *S. exigua* parasitized, suggesting that a constant 33°C decreases successful parasitization. In other parasitoid species oviposition trends were also inconsistent; increasing temperature could increase (Bezemer, Hefin Jones, and Knight 1998; Virtanen and Neuvonen 1999) or decrease rates of parasitism (Stireman et al. 2005).

Encapsulations of *C. marginiventris* immature stages were not impacted by temperature or selenium. This result indicates that temperature and selenium will not increase the susceptibility of *C. marginiventris* to greater mortality from this host immune response. Other studies regarding temperature effects on encapsulation rates of parasitoids within hosts have noted a variable relationship. Studies have reported increased encapsulation with increasing temperatures (Blumberg 1988, 1991), but the encapsulation rate can remain unaffected by temperature as well (Blumberg and DeBach 1979).

Selenium appeared to have no significant effects on fitness correlates of *C. marginiventris* in this study. This is in contrast to a previous study regarding the impact of selenium on parasitoids by Vickerman et al. (2004). In the previous study, negative consequences of selenium exposure included significantly longer development and decreases in pupal weight (Vickerman et al. 2004). An explanation for this contrast involves the amount of Se provided to hosts in their study (alfalfa contained on average  $327 \pm 21$   $\mu\text{g}$  Se/g dry weight, Vickerman et al. 2004) compared to our treatments with a maximum of  $44.48 \pm 0.59$   $\mu\text{g}$  Se/g dry weight of diet. The range of concentrations of Se in host plants of *S. exigua* ranges from nearly 0 to several thousand  $\mu\text{g}$ /g dry weight (Mikkelsen et al. 1989; Wu 1994), so both studies are within the ecological range likely to be encountered by *C. marginiventris*. However, even at this low level of Se provided to hosts in our experiments, Se still transferred from the host to *C. marginiventris*, but these levels did not affect the parasitoid. We suspect that *C. marginiventris* was exposed to a concentration of Se that was tolerated by the host or that the form of it present in the host larvae was less toxic to the parasitoid (which can occur through biotransformation mechanisms such as methylation, Vickerman et al. 2004). Additional research will be required to determine if either rationale is accurate.

In California, climatic models predict southern and central California will suffer substantial increases in temperatures (Diffenbaugh et al. 2008). Given the results of this study, *C. marginiventris* populations will experience decreased survival, and even surviving populations will experience decreased survival of their progeny. The life table statistics presented in our study also show decreased intrinsic rates of increase and net reproductive rates of the parasitoid at fluctuating temperatures, which would have profound consequences on this species' demography. However, the possibility exists that *C. marginiventris* may physiologically adapt to the predicted changes in

temperature and future studies could consider comparative adaptations of hosts and parasitoids that would affect their relative abilities to survive elevated temperatures. Increased temperatures have been reported to cause a decline in the cumulative morphospecies richness of parasitoids (Villapando et al. 2009), which indicates that at least some other parasitoid species have failed to adapt. In some locations *C. marginiventris* may be able to migrate into regions with cooler temperatures (higher elevations, etc.).

In the context of biological control and the use of parasitoids in an IPM program, temperature can have a strong impact on a parasitoid's development, reproduction, and survivorship (Messenger 1964; Bezemer et al. 1998). These effects have direct implications for optimizing mass rearing, improving field release techniques, selection of parasitoid species, and climate matching for successful establishment of agents (Lauziere, Setamou, Legaspi, and Jones 2002). The most common reason for failure in classical biological control projects is a poor climatic match between the native range of the parasitoid and region into which it is being introduced (ca. 35% of cases) (Stiling 1993). As the potentially detrimental impacts of climate change increase, herbivore outbreaks are predicted to increase due to a decrease in levels of parasitism by parasitoids in natural and managed systems (Stireman et al. 2005). Our research provides experimental evidence to support this hypothesis.

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