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Research

Reproductive Development of *Lygus hesperus* (Hemiptera: Miridae) Adults Under Constant and Variable Temperatures

Colin S. Brent[1] **and Dale W. Spurgeon**

Pest Management and Biocontrol Research Unit, USDA, ARS, ALARC, 21881 N Cardon Lane, Maricopa, AZ 85138, and [1]Corresponding author, e-mail: colin.brent@ars.usda.gov

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Abstract

As water for agriculture becomes less available in the semi-arid western United States, alternative irrigation strategies such as deficit irrigation may be necessary for continued crop production. Alternative irrigation practices in cotton (*Gossypium* spp. [Malvales: Valvaceae]) can result in episodic drought stress that alters temperature profiles within the crop canopy. These altered temperatures may influence populations of important pests such as *Lygus hesperus* Knight. Field studies often associate lower population densities of *L. hesperus* with limited irrigation. Recent studies of the thermal ecology of *L. hesperus* egg and nymphal development have demonstrated only subtle effects of the high, variable temperatures typical of moderate drought stress in cotton. However, influences of these conditions on *L. hesperus* adult reproductive development have not been studied. The reproductive development of *L. hesperus* adults was examined under constant (±0.2°C) and variable (±8°C) regimes at a low (15°C), moderate (22°C), and high (29°C) daily mean temperatures. No developmental differences were demonstrated between temperature regimes under moderate or high temperatures. At the low temperature, only the times to the occurrence of eggs, filled medial accessory glands, and filling seminal vesicles were shorter under variable regime, compared with the constant temperature. These results suggest that temporary, episodic increases in crop canopy temperatures caused by moderate drought stress are unlikely to impact *L. hesperus* population growth, and may only promote short-term displacement of adults into adjacent crops with preferable conditions.

Key words: temperature, development, reproduction

Agriculture of the semi-arid western United States is highly dependent upon the availability of affordable surface or ground water for irrigation. As water for agriculture becomes less available and more expensive, adoption of alternative water management methods such as deficit irrigation (González-Dugo et al. 2006, Mahan et al. 2012) may be necessary to maintain crop production. Under these alternative irrigation schemes, crops such as cotton (*Gossypium* spp. [Malvales: Malvaceae]) will experience periodic episodes of moderate drought stress. Plant canopy cooling by transpiration is dependent on soil moisture (Jackson et al. 1981, González-Dugo et al. 2006, Padhi et al. 2012). Therefore, episodic drought stress, combined with high air temperatures during the production season, may produce a thermal environment that is less favorable for pest and beneficial insects. Erratic precipitation and higher temperatures resulting from global warming are also likely to produce similar environmental effects.

The western tarnished plant bug, *Lygus hesperus* Knight is the most important pest of cotton in Arizona (Asiimwe et al. 2014). Studies of *L. hesperus* development and survival under constant temperatures have demonstrated both high- and low-temperature inhibition of egg and nymphal development (Cooper and Spurgeon 2012, 2013) and adult reproductive development (Spurgeon and Cooper 2012). Temperature is also known to influence survival of eggs and nymphs (Champlain and Butler 1967; Butler and Wardecker 1971; Cooper and Spurgeon 2012, 2013). Several field studies have reported a positive association between *L. hesperus* population densities and irrigation levels in cotton (Leigh et al. 1970; Flint et al. 1994, 1996; Asiimwe et al. 2014), suggesting that observed population responses were influenced at least in part by the effects of irrigation on crop canopy temperatures.

Temperature-dependent development rates under constant temperatures are often poorly representative of those observed under

variable temperatures (Hagstrum and Milliken 1991). Hagstrum and Milliken (1991) found that in many cases, variable temperatures moderated low-temperature inhibition of development, but slowed development under high-temperature conditions, compared with corresponding constant temperatures. Development of *L. hesperus* eggs and nymphs, and oviposition by adults, were recently compared under constant and variable temperatures (Spurgeon and Brent 2016, 2019; Brent and Spurgeon 2019). Those reports found modest increases in development times and mortality of nymphs and eggs at variable high temperatures, compared with constant temperatures. However, substantially higher rates of development and survival were associated with variable low temperatures compared with constant temperatures (Spurgeon and Brent 2016, 2019). In contrast, lifetime oviposition differed little whether the temperature regime was constant or variable, although oviposition rate, duration of the oviposition period, and female adult longevity varied among temperatures and between constant and variable regimes (Brent and Spurgeon 2019). Based on these collective results, Spurgeon and Brent (2019) suggested the responses of *L. hesperus* populations to irrigation levels in cotton were likely not caused by the effects of temporarily high temperatures on development and survival of eggs or nymphs. Instead, they suggested that when lower population densities of *L. hesperus* are associated with limited irrigation they likely result from host preferences by the mobile adults, or less deleterious effects of high canopy temperatures on the natural enemy complex. However, one potentially important aspect of *L. hesperus* thermal ecology that has not been documented is the reproductive development of adults in response to constant and variable temperatures. Our objective was to fill this knowledge gap using the same environmental conditions used in studies of the thermal ecology of other *L. hesperus* stages (Spurgeon and Brent 2016, 2019).

Materials and Methods

Experimental insects were the F_1 or F_2 progeny of adult *L. hesperus* collected from alfalfa (*Medicago sativa* L. [Fabales: Fabaceae]) near Maricopa, AZ. Parent adults were reared within 0.03-m^3 screened cages at 27 ± 1°C with a 14:10 h (L:D) photoperiod as described by Spurgeon and Brent (2019). Parents were provided pods of green bean (*Phaseolus vulgaris* L. [Fabales: Fabaceae]) as food and oviposition substrate, and raw seeds of sunflower (*Helianthus annuus* L. [Asterales: Asteraceae]). Nymphs hatching from bean pods were held on shredded paper within 4-liter plastic buckets with screened lids, where they received the same diet as the parent adults.

Once nymphs developed to fifth instars, their rearing buckets were examined three to five times daily to obtain newly eclosed adults. Newly eclosed adults were typically yellow to pale tan in color, and lacked the darker markings of older adults. Upon eclosion, each adult was confined to a separate 18-ml plastic vial (Thornton Plastics, Salt Lake City, UT) which was closed with a screened lid. Adults were fed sections of green bean pod (~5 cm in length) sealed on the cut ends with paraffin. At the lowest experimental temperature (15°C), bean sections were replaced twice weekly whereas they were replaced three times weekly at other temperatures (22 and 29°C).

An incomplete block design was used to examine combinations of three daily mean temperatures (15, 22, and 29°C) under constant (±0.2°C) and variable regimes (±8°C). Justification for temperature treatment selection is given in Brent and Spurgeon (2019). Corresponding constant and variable regimes at the same temperature were always included within the same experimental repetition. In each variable regime, the daily low temperature was maintained from 0200 h until 0600 h, then increased linearly to the daily high temperature by 1600 h. The high temperature was maintained until 2000 h, then decreased linearly to the daily low at 0200 h. The high variable temperature regime (mean = 29°C, range = 21–37°C) incorporated temperature extremes similar to those observed in field studies of moderately drought-stressed cotton (Wanjura et al. 2004, Carmo-Silva et al. 2012, Mahan et al. 2012, Sui et al. 2012). Temperature treatments were maintained within I30-BLL environmental chambers (Percival Scientific, Perry, IA) with a photoperiod of 14:10 h (L:D), and were monitored twice weekly using temperature loggers (U10-003, Onset Computer, Bourne, MA). The experiment was repeated (blocked) three times, yielding two replications of each temperature and regime combination. Because responses of male and female insects were based on different morphological characters, separate but concurrent experiments were conducted for each sex.

In each repetition of the experiment, 90–120 newly eclosed adults of each sex were assigned to each temperature and regime combination. Because sufficient numbers of adults were not available on a single day, adults were partitioned as evenly as possible among the treatment combinations as they became available. Development stage of the reproductive organs (ovaries in females; medial accessory glands and seminal vesicles in males) was assessed by serial dissection at intervals of 3-d of age for the low temperature, 2 d of age for the medium temperature, and daily for the high temperature. Ten males and 10 females were dissected at each designated age except for females at 27 d in the second repetition of the low constant temperature (n = 9), females at 24 d in the second repetition of the low variable temperature (n = 13), and males at 24 d in the first repetition of the low variable temperature (n = 9). In addition, nine males in the first repetition of the low variable temperature were inadvertently dissected at 13 d of age. Although dissections at that age were not planned, those data were included in the statistical analyses. In treatment combinations where mortality of adults was higher than expected, additional adults were assigned to facilitate dissections at 8–9 d (low temperature), 7 d (medium temperature), or 7–8 d (high temperature) age intervals or until all dissected adults exhibited maturity of the reproductive organs.

Dissections were performed as described by Spurgeon and Cooper (2012). Briefly, the insects were pinned through the prothorax into a saline-filled (0.7% NaCL [wt: vol]) depression in a paraffin-lined Petri plate, where the dorsal shield was removed. Development of female ovaries was classified by oocyte condition: 1) none, 2) previtellogenic oocytes (transparent and spherical), 3) vitellogenic oocytes (visible yolk accumulation), or 4) eggs. Eggs typically exhibited a pigmented operculum and a glossy surface indicative of a chorion. Medial accessory glands of males were classified as 1) undeveloped (small and transparent), 2) filling (translucent to opaque contents in the basal section of the gland but with conspicuous space between the visible contents and the gland periphery), or 3) filled (basal section of the glands conspicuously elongated with contents contacting most or all of the gland periphery and extending into the distal gland section). Seminal vesicles of males were classified as 1) undeveloped (transparent and filament-like), 2) filling (translucent to opaque contents but not filling the volume of the vesicle), or 3) filled (opaque contents filling the vesicle volume and extending through the encircling distal sections of the medial accessory glands).

The serial dissections provided data in the form of age-dependent frequency distributions for each developmental stage (Supp Figs. S1–S4 [online only]). For each combination of temperature, regime, sex, experimental repetition, and developmental stage, these frequency data were fitted to the equation logit(*age*) = *intercept* + *slope*(*age*) using

Firth's penalized logistic regression (the Firth option of the model statement in PROC LOGISTIC, SAS Institute 2012). Resulting model parameters were used to estimate the median time to development of each stage using the equation *age* = –(*intercept*/*slope*).

The estimated medians from the logistic regressions were inputs for analyses of the effects of temperature and regime for each combination of sex and development stage. The analyses included fixed effects of temperature, regime, and their interaction, and the random effect of experimental repetition. The analyses were performed using the GLIMMIX procedure of SAS (SAS Institute 2012). Due to the incomplete block design and variable sample sizes, denominator df were adjusted using the Kenward-Roger (DDFM = KR) option of the model statement. Where multiple comparisons were made among temperatures, the SIMULATE option of the LSMEANS statement was used to adjust for multiplicity. Where the temperature by regime interaction appeared significant, the source of the interaction was explored using simple effect tests (the SLICE option of the LSMEANS statement). The logistic regression equations describing the occurrence of filled seminal vesicles under the high variable temperature regime were exactly the same for both experimental repetitions (Supp Fig. S4 [online only]). Therefore, analysis of these data used a heterogeneous variances model to achieve estimates of the model parameters.

Results

All of the logistic regressions used to estimate median times to each development stage for both sexes were highly significant (Likelihood Ratio test, $P < 0.001$). Logistic regressions corresponding to duplicate repetitions of each combination of temperature, regime, development stage, and sex tended to become more similar as temperature increased and the time to attain each development stage decreased (Supp Figs. S1–S4 [online only]). This trend was expected because development times are extended by lower temperatures, thereby magnifying any differences between duplications of a treatment. All of the regression equations yielded biologically meaningful estimated medians for analyses of the effects of temperature and regime.

The median time to appearance of previtellogenic oocytes was dependent upon temperature, but temperature regime had no demonstrable effect (Table 1). The interaction between temperature and regime was not significant (Table 1), indicating the effects of temperature were similar under both constant and variable temperature regimes. Pairwise comparisons among temperatures indicated a reduced time to the presence of previtellogenic oocytes with each increase in temperature (Fig. 1a).

The occurrence of vitellogenic oocytes exhibited similar temperature dependency, and independence from temperature regime, as did the occurrence of previtellogenic oocytes (Table 1). Pairwise comparisons among the median times to occurrence of vitellogenic oocytes at different temperatures also indicated a simple decrease in time to this development stage with increasing temperature (Fig. 1b).

The influences of temperature and regime on occurrence of eggs were more complex compared with the influences on oocytes. While the effect of temperature was significant (Table 1), the temperature × regime interaction was not. However, simple effect tests of regime within temperatures indicated a difference in the median time to develop eggs at the lowest temperature (15°C, $F = 12.63$; df = 1, 4; $P = 0.024$), whereas no difference between regimes was indicated at 22°C ($F = 0.36$; df = 1, 4; $P = 0.583$) or 29°C ($F = 0.27$; df = 1, 4; $P = 0.632$). Simple effect tests within regime indicated a temperature effect for both the constant ($F = F = 77.12$; df = 2, 4.65; $P < 0.001$) and variable regimes ($F = 38.64$; df = 2, 4.65; $P = 0.001$). Pairwise comparisons among temperatures within regimes indicated a decreased time to develop eggs with increasing temperature under the constant regime (Fig. 1c). In contrast, the median time to presence of eggs was longest at the lowest temperature (15°C) under the variable regime, but no difference was demonstrated between the medium (22°C) and high (29°C) variable temperatures (Fig. 1c).

Temperature influenced the occurrence of filling male medial accessory glands, but neither the effects of regime nor the temperature × regime interaction were significant (Table 2). Comparisons among temperatures indicated the longest time to initiate filling of the accessory glands occurred at the lowest temperature (15°C), and differences between 22 and 29°C were too small to demonstrate after adjustment for multiplicity (Fig. 2a). In contrast, analysis of the median time to filled accessory glands indicated a significant temperature × regime interaction, suggesting the effects of regime were conditional on temperature (Table 2). Although the time required to fill the medial accessory glands decreased with increasing temperature for both regimes (constant, $F = 228.00$; df = 2, 4.24; $P < 0.001$; variable, $F = 95.46$; df = 2, 4.24; $P < 0.001$; Fig. 2b), regimes differed at the lowest temperature when development was more rapid under the variable regime (15°C, $F = 44.67$; df = 1, 4; $P = 0.003$; 22°C, $F = 0.03$; df = 1, 4; $P = 0.874$; 29°C, $F = 1.30$; df = 1, 4; $P = 0.318$).

The pattern of occurrence of filling seminal vesicles was similar to that of filled accessory glands, with a significant temperature × regime interaction (Table 2). Simple effect tests of temperature within regime indicated decreasing time to filling seminal vesicles with increasing temperature under both regimes (constant, $F = 346.31$; df = 2, 4.52; $P < 0.001$; variable, $F = 148.42$; df = 2, 4.52; $P < 0.001$), and this pattern remained after pairwise comparisons were adjusted for multiplicity (Fig. 2c). However, at the lowest temperature, development occurred more rapidly under the variable regime compared with the constant temperature (15°C, $F = 90.19$; df = 1, 4; $P < 0.001$;

Table 1. Tests of model effects assessing the median time to occurrence of reproductive development stages for female *Lygus hesperus* at combinations of three daily mean temperatures (15, 22, and 29°C) and two temperature regimes (constant, ±0.2°C; variable, ±8°C)

Development stage	Model effect	*F*	df	*P*
Previtellogenic oocyte	Temperature	85.87	2, 4.52	<0.001
	Regime	0.79	1, 4	0.424
	Temperature × regime	0.39	2, 4	0.699
Vitellogenic oocyte	Temperature	74.90	2, 4.73	<0.001
	Regime	2.51	1, 4	0.188
	Temperature × regime	0.92	2, 4	0.468
Egg	Temperature	89.79	2, 5.19	<0.001
	Regime	4.40	1, 4	0.104
	Temperature × regime	4.43	2, 4	0.097

22°C, F = 1.37; df = 1, 4; P = 0.307; 29°C, F = 0.01; df = 1, 4; P = 0.937).

Although the temperature- and regime-dependent patterns of occurrence of filled seminal vesicles were superficially similar to those of the other development stages, only a significant temperature effect was detected (Table 2). Furthermore, pairwise comparisons among the temperatures revealed clear differences only between the lowest (15°C) and highest (29°C) temperatures (Fig. 2d).

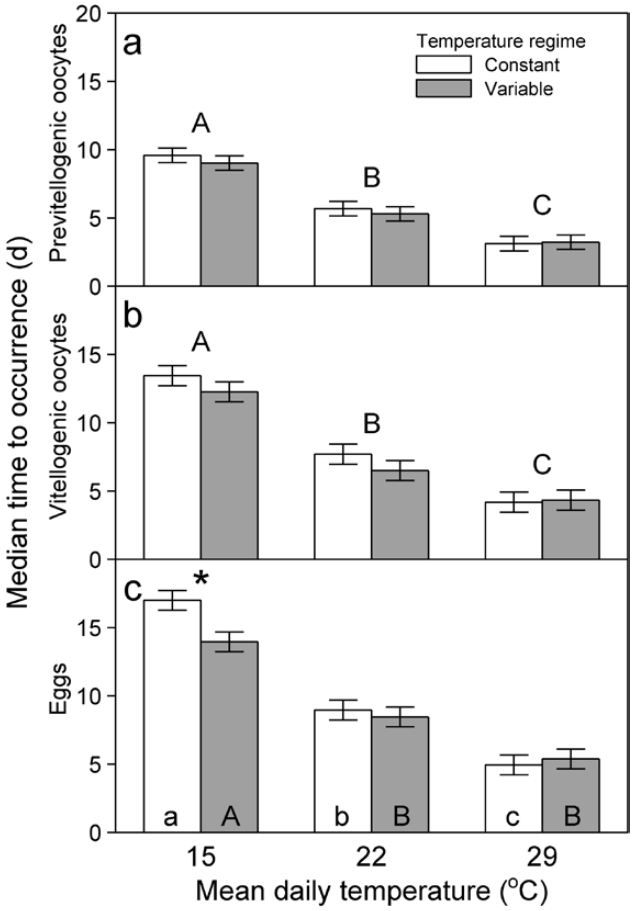

Fig. 1. Mean (±SE) of the median times to occurrence of previtellogenic oocytes (a), vitellogenic oocytes (b), and eggs (c) in adult female *L. hesperus* held under constant (±0.2°C) and variable (±8°C) temperature regimes with a photoperiod of 14:10 h (L:D). Paired bars within a daily temperature marked by an asterisk (*) indicate a significant difference ($\alpha < 0.05$) between temperature regimes. Bars within a developmental stage marked by the same lowercase (constant temperature) or uppercase letter (variable temperature) are not significantly different at experiment-wise $\alpha = 0.05$.

Discussion

The influences of temperature and temperature regime on adult *L. hesperus* reproductive development exhibited patterns similar to those observed for nymphs developing under the same experimental treatments (Spurgeon and Brent 2019). The primary difference between the two studies occurred in the results for the high temperature treatments. For most nymphal instars, Spurgeon and Brent (2019) showed significant, albeit small, increases in development times under the variable regime compared with the constant high temperature. Although similar numerical trends were observed for most reproductive development stages in adults, there were no statistical differences.

For female *L. hesperus*, the more rapid rate of egg maturation found with increasing temperature corresponded to the previously observed reduction in preoviposition period for females reared at higher temperatures (Brent and Spurgeon 2019). As with that earlier study, a difference between temperature regimes was observed for the occurrence of eggs at the lowest temperature, but not for the occurrence of previtellogenic or vitellogenic oocytes. The relative rapidity of initial oocyte development may be responsible for this apparent discrepancy. Likewise, absence of demonstrable differences between temperature regimes at higher temperatures was probably caused by the short development times at those temperatures. Such limited responses would only cause a slight delay in the onset of female mating and oviposition, behaviors that are tightly coordinated with the availability of mature eggs (Brent 2010a).

A similar pattern of response was observed for the development of the medial accessory glands in males, where an influence of temperature regime was only observed for the most mature development stage at the lowest temperature. In contrast, a difference between regimes was observed for the initiation of filling of the seminal vesicles at the lowest temperature, whereas no difference was observed for the completion of filling. This suggests the low temperatures influenced the initiation of seminal vesicle filling more than they influenced the subsequent rate of filling. Although the development of the medial accessory glands and seminal vesicles are both sensitive to low-temperature inhibition, Spurgeon and Cooper (2012) reported that their development is often not well synchronized. Diapause

Table 2. Tests of model effects assessing the median time to occurrence of reproductive development stages for male *Lygus hesperus* at combinations of three daily mean temperatures (15, 22, and 29°C) and two temperature regimes (constant, ±0.2°C; variable, ±8°C)

Development stage	Model effect	F	df	P
Filling medial accessory glands	Temperature	19.80	2, 4.80	0.005
	Regime	1.62	1, 4	0.272
	Temperature × regime	2.38	2, 4	0.209
Filled medial accessory glands	Temperature	260.15	2, 4.42	<0.001
	Regime	10.88	1, 4	0.030
	Temperature × regime	17.56	2, 4	0.010
Filling seminal vesicles	Temperature	384.07	2, 4.95	<0.001
	Regime	37.33	1, 4	0.004
	Temperature × regime	27.12	2, 4	0.005
Filled seminal vesicles[a]	Temperature	224.24	2, 1	0.047
	Regime	0.34	1, 3	0.601
	Temperature × regime	1.34	2, 3	0.384

[a]Denominator degrees of freedom are reduced because the analysis used a heterogeneous variances model.

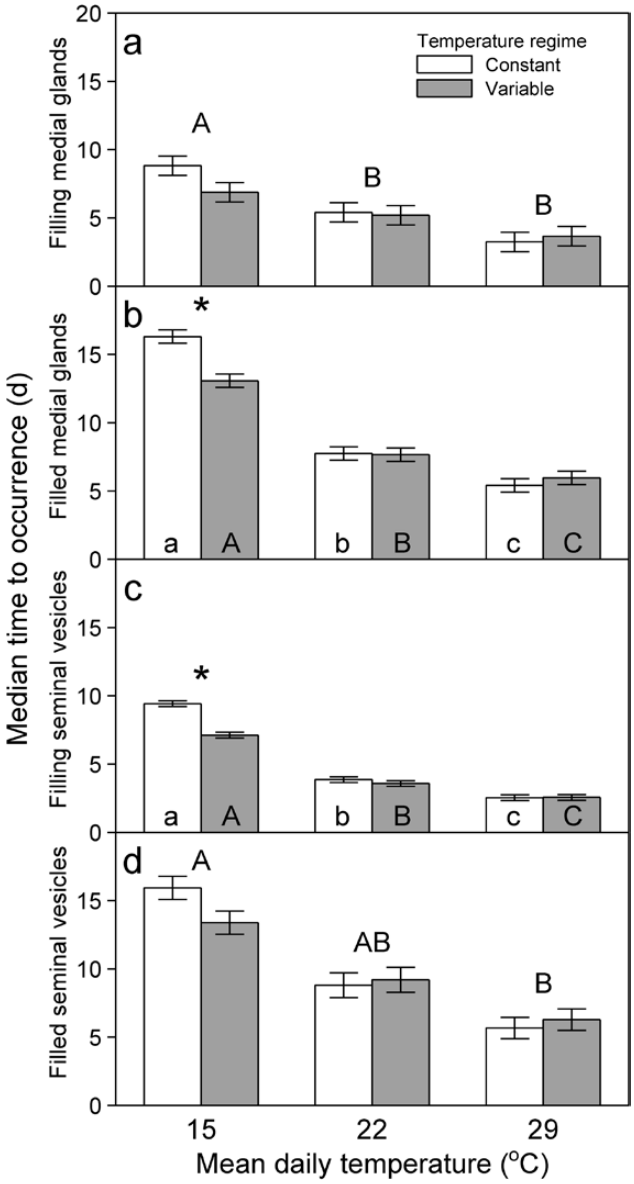

Fig. 2. Mean (±SE) of the median times to occurrence of filling medial accessory glands (a), filled medial accessory glands (b), filling seminal vesicles (c), and filled seminal vesicles (d) in adult male *L. hesperus* held under constant (±0.2°C) and variable (±8°C) temperature regimes with a photoperiod of 14:10 h (L:D). Paired bars within a daily temperature marked by an asterisk (*) indicate a significant difference ($\alpha < 0.05$) between temperature regimes. Bars within a developmental stage marked by the same lowercase (constant temperature) or uppercase letter (variable temperature) are not significantly different at experiment-wise $\alpha = 0.05$.

studies have also demonstrated a lack of synchrony in development of the medial accessory glands and seminal vesicles, because diapause induction inhibits the development of the accessory glands but has little effect on development of the seminal vesicles (Spurgeon and Brent 2010). Our results are consistent with the observations of Spurgeon and Cooper (2012), suggesting different temperature-dependent mechanisms are mediating the development of the two organ systems. Regardless, the small responses to temperature and regime would have limited impact on the timing of initial mating (Brent 2010a) and possibly the duration of the post-mating refractory period (Brent 2010b), when these organs are being refilled.

The small effects of variable temperatures that were observed under the highest temperature suggest that temporary, episodic exposure to unfavorably high canopy temperatures like those typical of moderate drought stress would have little impact on *L. hesperus* reproduction in the field. This conclusion is consistent with the suggestion by Spurgeon and Brent (2019) that associations of lower *L. hesperus* population densities with limited irrigation are likely caused by the reactions of immigrating vagile adults dispersing away from suboptimal conditions rather than by the deleterious effects of high canopy temperatures. In that case, the population responses to irrigation level observed in previous reports (Leigh et al. 1970; Flint et al. 1994, 1996; Asiimwe et al. 2014) may have been facilitated by the relatively small plot sizes and presence of well-irrigated alternatives, compared with commercial production where whole fields may exhibit moderate drought stress with few or no nearby alternatives. These results suggest that efforts to manipulate *L. hesperus* populations by altering the thermal environment of the host may be of limited usefulness without additional study of host preferences or host selection by immigrating *L. hesperus* adults. Further, the near-term impact of global warming on the growth and distribution of this Arizona population of heat-tolerant *Lygus* should be minimal. However, populations adapted to cooler thermal conditions might have more pronounced responses.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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