Egg Production and Longevity of *Lygus hesperus* (Hemiptera: Miridae) Adult Females Under Constant and Variable Temperatures[1]

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Abstract Changing irrigation practices and rising global temperatures will impact pest insect populations, but limited knowledge of the thermal ecology of individual species prevents accurate modeling of their likely responses. Most studies focusing on temperature responses of the western tarnished plant bug, *Lygus hesperus* Knight (Hemiptera: Miridae), a major pest of cotton (*Gossypium* spp.), have been limited to constant conditions, whose relevance to the variable temperatures of field environments is unknown. To address this, newly emerged adults of *L. hesperus* were reared under environmentally relevant low (mean, 15°C), medium (mean, 22°C), or high (mean, 29°C) constant (±<0.5°C) or diurnally fluctuating (±8°C) temperatures. Females under the warmest conditions produced eggs sooner and at a faster rate than those reared under the coolest conditions but also had reduced lifespans. Variable temperatures shortened the preoviposition period under cool conditions and lengthened the duration under high heat. Lifetime egg production was unaffected by temperature regime. The adaptive responses of adult *L. hesperus* to environmental temperature indicate that implementing a control strategy that uses the thermal stress created by deficit irrigation may be difficult, although other developmental stages of this pest may be more susceptible.

Key Words adult maturation, oviposition, *Lygus hesperus*, western tarnished plant bug, thermoperiod

Temperature influences all aspects of insect life history (Campbell et al. 1974, Taylor 1981), but the precise effects vary widely by species, developmental stage, and previous thermal experiences. The picture is further complicated by the ability of many insects to shelter within the crop canopy, which is typically cooler than ambient because of evapotranspiration (Carmo-Silva et al. 2012, Sui et al. 2012). Crop canopies can provide a critical refuge for many key pests in the southwestern United States, where peak air temperatures can exceed their survival limits. Because canopy cooling is dependent on the availability of soil moisture (González-Dugo et al. 2006, Jackson et al. 1981, Jackson 1982, Padhi et al. 2012), adoption of alternative irrigation methods, such as deficit irrigation (González-Dugo et al. 2006, Mahan et al. 2012), might impact pest populations. Developing approaches to

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predict and exploit such impacts to better manage pests will require substantial knowledge of insect thermal ecology and physiology.

The western tarnished plant bug *Lygus hesperus* Knight is an abundant pest of numerous crops throughout the southwestern United States (Clancy and Pierce 1966, Slosser et al. 2006) and causes significant economic impact for cotton (*Gossypium* sp.) in Arizona (Ellsworth 1998, Ellsworth and Jones 2001, Fournier et al. 2007). Higher *Lygus* population levels are often associated with ample irrigation compared with population levels observed when plants exhibit moderate drought stress (Asiimwe et al. 2014, Flint et al. 1994, 1996, Leigh et al. 1970, Munk and Goodell 2002). However, it is not clear whether these are thermal effects or merely indicate the preferences of mobile adults. Relationships between temperature and development of *L. hesperus* eggs and nymphs have been described by linear regression (Champlain and Butler 1967, Butler and Wardecker 1971) and more recently by using the nonlinear model of Sharpe and DeMichele (1977), as modified by Schoolfield et al. (1981) (Cooper and Spurgeon 2012, 2013). Early reports of temperature dependence of adult reproductive development were based on preoviposition times (Beards and Leigh 1960, Leigh 1963, Strong et al. 1970, Strong and Sheldahl 1970). More recent examinations were based on direct observation of reproductive morphology either at a single temperature (Brent 2010) or over a range of temperatures (Spurgeon and Cooper 2012). The most recent studies (Cooper and Spurgeon 2012, 2013; Spurgeon and Cooper 2012) have generally indicated the presence of both low- and high-temperature inhibition of development, the extent of which varied among *L. hesperus* stages and instars.

Hagstrum and Milliken (1991) cited numerous examples in which development under variable high temperatures was slower than under corresponding constant temperatures, whereas the opposite was true at lower temperatures. They also reported that the amplitude of the variable temperature regime influenced development time. In contrast, Champlain and Butler (1967) reported that development times of *L. hesperus* eggs under constant and variable temperatures did not differ, and Butler and Watson (1974) reported that development rates of *L. hesperus* stages under constant temperatures were predictive of development times under variable temperatures. However, variable low temperatures were found to hasten *L. hesperus* egg development and increase survival, whereas variable high temperatures delayed development and reduced survival compared with constant temperature regimes (Spurgeon and Brent 2016). This finding supports the trends reported by Hagstrum and Milliken (1991) and suggests that other developmental stages of *L. hesperus* might exhibit differential responses to variable and constant temperatures.

Previous studies of egg production and longevity of adult *L. hesperus* in response to constant (Mueller and Stern 1973) and variable temperatures (Strong and Sheldahl 1970) used thermal regimes with limited relevance to field environments. Furthermore, by pairing maturing females with males, the results of these previous studies are confounded by male-specific stimuli that have been shown to strongly impact both fecundity and survivorship (Brent et al. 2011, Brent 2018). These pronounced effects could obscure physiological responses to temperature regime. Having a predictive understanding of population dynamics and being able to anticipate likely impacts of alternative irrigation schemes will require a more accurate assessment of the effects of thermal environment than

current data provide. Toward that end, we investigated *L. hesperus* egg production and longevity under ecologically meaningful, variable temperatures without a male present.

Materials and Methods

Insects. Test subjects were the F_1 or F_2 progeny of 400–500 adult *L. hesperus* collected from alfalfa (*Medicago sativa* L.) near Maricopa, AZ. Field collections were made in October and November 2017. As previously described (Spurgeon and Brent 2015), collected adults were maintained in incubators set at 27.0 ± 1°C with a photoperiod of 14:10 (light [L]:dark [D]) h. They were held in collapsible cages (30.5 × 30.5 × 30.5 cm; BioQuip, Rancho Dominguez, CA) provisioned with shredded paper and a sheet of Hexcel (PN1, Hexcel, Pleasanton, CA) for refuge and saturated cotton as a water source. The insects were fed raw sunflower seeds (*Helianthus annuus* L.) and fresh green bean pods (*Phaseolus vulgaris* L.) three times weekly. At each feeding, the pods that were replaced, which contained newly oviposited eggs, were transferred to a 4-L plastic bucket. The bucket contained shredded paper and a sheet of Hexcel and was closed with a screened lid. Hatched nymphs were provided the same diet as the parent colony and were held within the rearing buckets until adult eclosion. Beginning when fifth instars were observed, rearing buckets were inspected daily for newly eclosed adults, which were removed from the buckets. Adult females eclosing each subsequent day (0 to 1 d old) were collected and assigned to temperature treatments.

Oviposition and longevity. To determine the effects of temperature on oviposition rates and longevity, a randomized incomplete block experimental design was used. Each treatment combination of temperature (15°C, 22°C, 29°C, ±0.5°C) and temperature regime (constant and variable) was represented by two replications distributed among three experimental repetitions (blocks). Each replication of each treatment combination was represented by a cohort of 35 *L. hesperus*. The respective cohorts were the experimental units. The insects were newly emerged virgin adult females, housed individually in 1.5 × 5.0-cm plastic petri dishes supplied with a 2- to 3-cm section of green bean and two sunflower seeds. Beans were replaced daily and seeds as needed.

Dishes were maintained in environmental chambers (I30BLL; Percival Scientific, Perry, IA) with a 14:10 (L:D)-h photoperiod. The six thermal treatments consisted of (1) "low variable" (7–23°C; mean, 15°C), (2) "low constant" (15°C), (3) "medium variable" (14–30°C; mean, 22°C), (4) "medium constant" (22°C), (5) "high variable" (21–37°C; mean, 29°C), and (6) "high constant" (29°C). The mean temperature and amplitude of the high variable treatment were selected based on reports of cotton canopy temperatures during moderate drought stress (Wanjura et al. 2004, Carmo-Silva et al. 2012, Mahan et al. 2012, Sui et al. 2012). Amplitudes of the medium variable and low variable regimes (±8°C) were the same as for the high-variable regime because Hagstrum and Milliken (1991) reported both mean temperature and amplitude influenced insect development time. The mean temperature of the medium-variable regime was selected so the daily temperature range was contained within the portion of the *L. hesperus* temperature-dependent ovary development rate curve that is approximately linear (Spurgeon and Cooper 2012).

The mean and amplitude of the low-variable regime are typical of conditions in Central Arizona during the late fall and early spring (http://www.usclimatedata.com), when the daily low temperature is below the estimated lower thermal threshold for *Lygus* ovarian development (Spurgeon and Cooper 2012).

Each temperature treatment was assigned to a separate environmental chamber, and treatments within a repetition (block) were run concurrently. In each variable temperature regime, the low temperature was maintained from 0200 h until the chamber lights were started (0600 h). Temperature was then increased linearly to the high temperature by 1600 h, where it was maintained until the chamber lights were stopped (2000 h), and then decreased linearly to the low temperature by 0200 h. Thus, warming and high temperatures occurred during the 14-h photophase, while declining and low temperatures occurred during the 10-h scotophase. Chamber temperatures were monitored using portable loggers (U10-003; Onset Computer, Bourne, MA), from which data were collected at least twice weekly. Temperature offsets on the environmental chambers were adjusted to ensure that low, high, and mean temperatures in the variable temperature regime and mean temperatures in the constant temperature regimes were maintained within ± 0.5°C of the desired setting.

A daily census assessed female survivorship and the number of eggs laid in the green bean section during the preceding 24 h. A dissecting stereomicroscope was used to count eggs. The census was continued for each treatment until all females had perished, although the experiment was terminated early in one repetition of the low-constant regime when one female had survived to 200 d.

Statistics. All analyses were performed using SAS (SAS 2012). Because of considerable variation in female lifespan and propensity to oviposit, both among and within treatments, we characterized the treatment effects on total lifetime oviposition, probability of oviposition, lifetime oviposition rate (eggs female^{-1} d^{-1}), durations of respective preoviposition and oviposition periods, and survival rates. Analyses of the probability of oviposition and of female survival included all females; remaining analyses included only females that oviposited at least once. Wherever multiple comparisons were made of more than two means, corresponding *P* values were adjusted for multiplicity using the SIMULATE option. Where analyses involved non-Gaussian distributions, means on the data scale were obtained using the ILINK option.

Analysis of treatment effects on total lifetime oviposition used a linear mixed model with heterogeneous variances for each temperature. Fixed effects included temperature, regime, and their interaction. Repetition of the experiment (block) was a random effect. In addition, the repetition $\times$ temperature $\times$ regime interaction was random and served as the error term for tests of the fixed effects. Degrees of freedom were corrected using the DDFM=KR option of the model statement.

Analyses of oviposition rate used data for individual females but were calculated to represent the experimental unit (cohort of females). Therefore, estimates of lifetime oviposition rate for individual females were calculated as the total number of eggs laid divided by the lifetime of the cohort, instead of the lifetime of each female. This approach best represented the cohort and avoided inflating the apparent oviposition rate when a few females were unusually fecund or produced eggs for an extended duration. Analysis of lifetime oviposition rate used the same model as for total oviposition.

Examinations of the probability of oviposition used a conditional model with Laplace estimation and a binomial distribution. Fixed effects included temperature, regime, and their interaction, and repetition of the experiment was a random effect. Because the analysis used events and trials syntax, residual served as the error term for tests of fixed effects.

Analyses of the durations of respective preoviposition and oviposition periods used conditional models with Laplace estimation and negative binomial distributions. Fixed effects included temperature, regime, and their interaction, and random effects included repetition of the experiment and the repetition $\times$ temperature $\times$ regime interaction. Duration of oviposition was calculated as the insect's age on the last day of oviposition minus the preoviposition period. Where the temperature $\times$ regime interaction appeared nonnegligible, effects of treatment combinations were examined using simple effect tests (Stroup 2013).

Survival functions corresponding to each combination of temperature and regime were compared using the log-rank χ^2 statistic of the LIFETEST procedure. This analysis was stratified by (adjusted for) experimental repetition, and 95% confidence limits were calculated for each treatment combination.

Results

Oviposition. Of the 420 insects examined, only 254 (60.5%) oviposited before dying. The probability that a female would oviposit (Fig. 1A) was influenced by mean temperature ($F = 10.38$; df $= 2, 4$; $P = 0.03$) but not regime ($F = 2.32$; df $= 1, 4$; $P = 0.20$). No interaction was detected between these variables ($F = 1.86$; df $= 2, 4$; $P = 0.27$). The probability of oviposition was highest at the medium temperature (22°C) and lowest at the high temperature (29°C; adjusted [adj.] $P = 0.02$). The probability of oviposition at the lowest temperature (15°C) was intermediate to, and not different from, that at the other temperatures ($0.14 \leq$ adj. $P \leq 0.19$; Fig. 1A).

The timing of oviposition initiation (Fig. 1B) was impacted by mean temperature ($F = 203.30$; df $= 2, 4$; $P < 0.01$) but not regime ($F < 0.01$; df $= 1, 4$; $P = 0.97$). However, a significant interaction effect indicated that the influence of temperature varied by regime ($F = 17.99$; df $= 2, 4$; $P = 0.01$; Table 1). Simple effect tests comparing regimes within temperatures indicated that the preoviposition period for the variable regime was shorter than for the constant regime at 15°C ($F = 30.57$; df $= 1, 4$; $P < 0.01$), whereas the period for the variable regime was longer than for the constant regime at 29°C ($F = 10.89$; df $= 1, 4$; $P = 0.03$). In contrast, no influence of regime was demonstrated at the medium temperature ($F < 0.01$; df $= 1, 4$; $P = 0.97$). Multiple comparisons among temperatures indicated that preoviposition time decreased as temperature increased under the constant regime (adj. $P < 0.01$). A similar response was observed for the variable regime, except there was no difference between 22°C and 29°C after correcting for multiplicity (adj. $P = 0.07$).

The amount of lifetime spent ovipositing (Fig. Fig. 1C) was also influenced by temperature ($F = 19.08$; df $= 2, 4$; $P < 0.01$) but not by regime ($F = 3.29$; df $= 1, 4$; $P = 0.14$). There was also no interaction effect ($F = 0.34$; df $= 2, 4$; $P = 0.73$). Females reared at 15°C oviposited longer than those reared at 22°C (adj. $P = 0.03$) or 29°C (adj. $P < 0.01$). There was no difference between the latter groups (adj. $P = 0.16$).

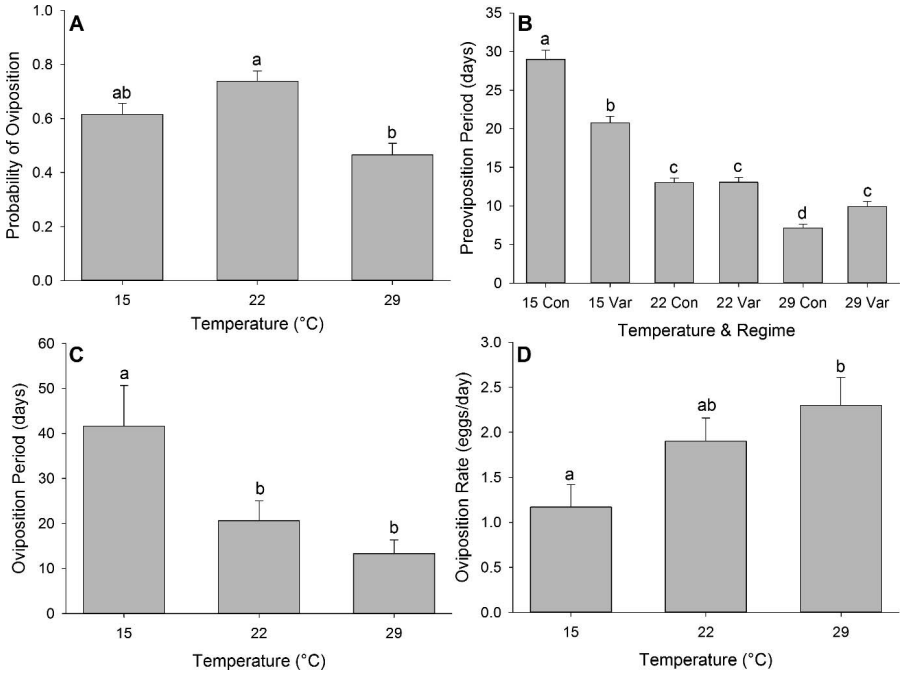

Fig. 1. Reproductive parameters of *Lygus hesperus* adult females exposed to constant (±<0.5°C) and variable (±8°C) temperature regimes; probability of oviposition under three temperatures (A), preoviposition period under combinations of three temperatures and constant or variable regimes (B), duration of the oviposition period under three temperatures (C), and daily oviposition rate under three temperatures. Bars under the same letters within a panel are not significantly different after adjustment for multplicity (experimentwise $\alpha = 0.05$).

The rate of oviposition (Fig. 1D) was also significantly affected by temperature ($F = 14.05$; df = 2, 77.13; $P < 0.01$) but not regime ($F = 2.71$; df = 1, 140.8; $P = 0.10$), and there was no interaction effect ($F = 1.92$; df = 2, 88.07; $P = 0.15$). Oviposition rate was lower for those reared at 15°C than for those at 22°C (adj. $P < 0.01$) or 29°C (adj. $P < 0.01$). There was no difference in the rates for the latter two groups (adj. $P = 0.43$). Despite rate differences among treatments, lifetime fecundity (Fig. 2) was not affected by temperature ($F = 3.59$; df = 2, 1; $P = 0.35$), regime ($F = 0.65$; df = 1, 1.32; $P = 0.54$), or interaction between the variables ($F = 0.28$; df = 2, 1; $P = 0.80$).

Longevity. Treatment caused differential survivorship among lygus insects (log-rank χ^2, 109.52; df = 5; P < 0.01; Fig. 3). Pairwise comparisons between constant and variable regimes within temperatures did not indicate significant differences in longevity (0.06 ≤ adj. $P \leq 1.00$). Comparisons among temperatures within the constant regime did not indicate a difference in longevity between females held at 15°C and 22°C (adj. $P = 0.06$), but longevity at 15 and 22°C was longer than at 29°C

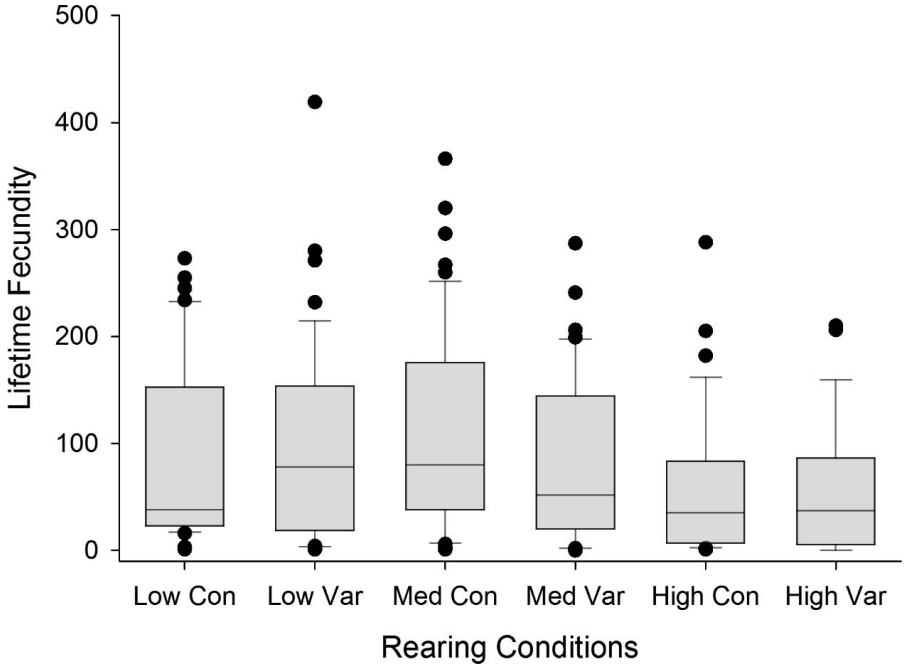

Fig. 2. Lifetime oviposition of adult female *L. hesperus* developing under combinations of three temperatures (15°C, 22°C, and 29°C) and either constant (±<0.5°C) or variable (±8°C) temperature regimes. Presented are the medians, interquartile ranges, 90th and 10th percentiles (whiskers), and any outlier data points exceeding these outer bounds (black circles).

(adj. $P < 0.01$). Under the variable regime, longevity was greater at 15°C than at either 22°C or 29°C (adj. $P < 0.01$), but longevity at 22°C and 29°C was not different (adj. $P = 0.843$).

Discussion

Although relatively lower *L. hesperus* population levels in cotton are often associated with limited irrigation compared with ample irrigation (Asiimwe et al. 2014, Flint et al. 1996, Munk and Goodell 2002), the mechanisms responsible for the population responses have not been identified. Because reduced water availability can induce an increase in canopy temperature (González-Dugo et al. 2006, Jackson et al. 1981, Padhi et al. 2012), drought stress tends to expose resident insects to potentially adverse thermal conditions that may influence development, survival, or reproduction. Alternatively, if *L. hesperus* exhibits adaptations that sufficiently limit the deleterious impacts of thermal stress, then previously observed population responses to variations in crop water status may simply indicate the environmental preferences of the mobile adult stage. In that

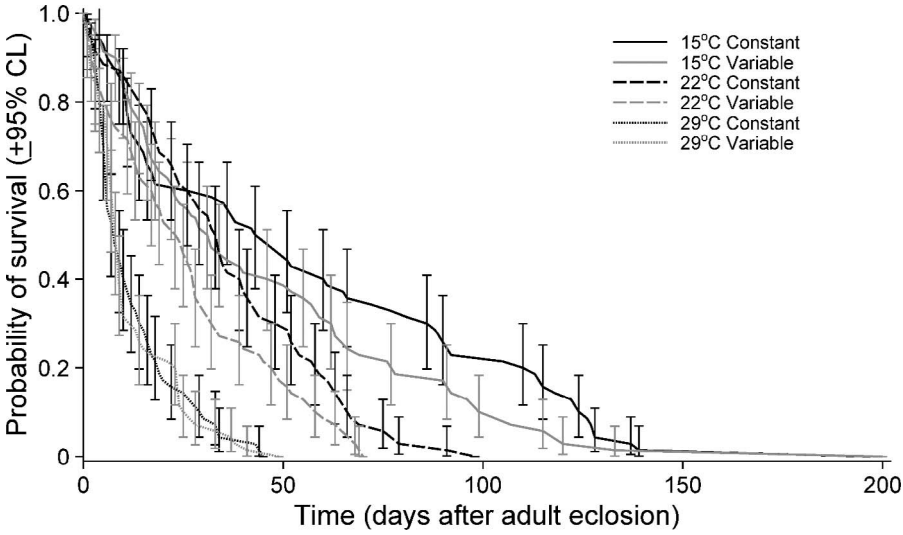

Fig. 3. Survival functions for adult female *L. hesperus* females held under combinations of three temperatures (15°C, 22°C, and 29°C) and either a constant (±0.5°C) or variable (±8°C) temperature regime. Confidence intervals are provided only at selected intervals for clarity.

case, the population responses observed in small-plot studies (essentially, choice tests) may not be widely applicable to the larger production system where choices among fields are limited by distance or lack of diversity in crop water status.

Under a range of environmentally relevant temperatures, we observed that females in the warmest conditions produced eggs sooner and at a faster rate and had shorter lifespans than those reared in the coolest conditions. These results are consistent with previous findings for this and other species of *Lygus* (Strong et al. 1970, Strong and Sheldahl 1970, Bryan et al. 1976, Khattat and Stewart 1977, Men et al. 2008, Cooper and Spurgeon 2012, Spurgeon and Cooper 2012, Ugine 2012). The effects of temperature regime were less pronounced but were still consistent with previous findings for lygus eggs (Spurgeon and Brent 2016) and for a range of other species (Hagstrum and Milliken 1991), in which low but variable temperatures enhance development compared with low-constant temperatures, whereas the opposite was observed when temperatures were high. In our current study, differences between regime responses were manifested only through changes to the duration of the preoviposition period, with a prolongation at high- and a shortening at low-variable temperatures relative to constant conditions. These divergent responses are likely the result of differential allocation of resources toward somatic maintenance and vitellogenesis, as determined by the level of thermal stress (Neven 2000, De Maio et al. 2012). However, influences of our experimental conditions on the probability, duration, and rate of oviposition and on adult longevity were explained by differences in mean temperatures without respect to whether those temperatures were constant or variable. Most notably, neither

temperature nor temperature regime influenced total lifetime oviposition in a statistically demonstrable fashion.

Lygus hesperus exhibits a wide host range (Scott 1977) and a geographic distribution from northern Mexico into Canada (Kelton 1975). These factors imply the species has a marked ability to adapt to a range of conditions, either through individual or population-based genetic heterogeneity. Such heterogeneity, and amenability to adaptation, is evident in the incidence of diapause; long-term laboratory rearing is associated with a diminished diapause response (Spurgeon 2012), and only a portion of some field populations exhibit diapause (Spurgeon and Brent 2015). In central Arizona, a substantial fraction of the overwintering *L. hesperus* population remains reproductive (Spurgeon and Brent 2015, Spurgeon 2017). Shortening of the preoviposition period under variable low temperatures (about 75% of the duration compared with low constant temperature) may facilitate population maintenance or growth during winters when wild or cultivated hosts remain suitable for reproduction.

Lygus hesperus adults are known to express a variety of genes in response to xenobiotic and biotic stressors (Hull et al. 2014), including the upregulation of specific heat-shock proteins in response to thermal stress (Hull et al. 2013). Therefore, the relatively subtle responses of ovipositing females to constant versus variable temperatures and the lack of a substantial overall effect of temperature on lifetime oviposition may be linked to the activity of stress-induced genes that ameliorate the otherwise deleterious impacts of thermal extremes. Irrespective of the specific mechanisms by which *L. hesperus* cope with thermal stress, the magnitudes of the responses we observed, in the absence of contradicting field-based evidence, seem unlikely to produce marked population responses to short-term high- or low-temperature stressors. However, it is still possible that the observed population responses might be explained by the effects of variable high or low temperatures on nymphal development or survival by impacts on mating success mediated through the effects of thermal stress on reproductive development of males or by increased impacts of natural enemies less responsive to temperature extremes than their *Lygus* prey. Our results provide an incremental but important contribution to further understanding the interactions between *L. hesperus* and the thermally inhospitable environment of southwestern agriculture.

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