Stage-dependent feeding behavior by western tarnished plant bugs influences flower bud abscission in cotton

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Abstract

Unexplained variability in the relationship between the number of herbivores in a field and the amount of crop damage can arise if there is a large amount of variation among herbivore individuals in the amount of feeding damage each generates. In California, populations of the western tarnished plant bug, *Lygus hesperus* Knight (Heteroptera: Miridae), produce highly variable levels of damage to cotton plants (*Gossypium hirsutum* L.) (Malvaceae), even when found at low densities. Because *L. hesperus* populations are also highly variable in their overall stage structure, we hypothesize that differences in crop damage might result from varying impact by each *L. hesperus* stage on cotton flower buds (termed squares). Laboratory measurements of *L. hesperus* mouth-parts and distance to anther sacs, a preferred feeding site, revealed that 1st–3rd instar *L. hesperus* nymphs will not be able to feed on anther sacs of larger squares (over 8 mm in length) but will be able to feed on squares that are most sensitive to *L. hesperus* damage (<7 mm). Because even the 1st instars can feed on the most sensitive 'pinhead' squares, size constraints do not rule out damaging effects from the youngest *L. hesperus*. Laboratory observations revealed that later developmental stages, and adults, spend more time feeding on cotton squares relative to 2nd and 3rd instars. In addition, a field experiment revealed no effect of 2nd instars on square retention (relative to control cages) but did reveal a significant decrease in square retention generated by adult *L. hesperus* (4th instar *L. hesperus* resulted in an intermediate level of square retention). In a final study we sampled *L. hesperus* stage structure and density across 38 cotton fields. Multiple regression revealed that the densities of 1st–3rd instars of *L. hesperus* are not correlated with anther sac damage or square retention. However, in 2 years 4th and 5th instars were positively correlated with anther sac damage and negatively correlated with square retention. In the a third year, adult *L. hesperus* showed correlations in the same direction, across fields and across sites within fields. Overall, these results suggest that the adults and the largest nymphs of *L. hesperus* (4th and 5th instars) are particularly damaging to cotton squares, with the 1st–3rd instars of *L. hesperus* causing little damage to plants.

Introduction

When insect pests exhibit stage-dependent feeding behavior, variation in the stage structure of a local pest population is likely to produce a unique signature of damage across different fields. Therefore, the characterization of stage-dependent feeding behavior can be an important component of integrated pest management. However, for many pests the behaviors of particular life stages are difficult to observe due to frequent movement or cryptic feeding. Field-based focal observations have revealed that nymphs of the western tarnished plant bug, *Lygus hesperus* Knight (Heteroptera: Miridae), often feed cryptically beneath the bracts of cotton (*Gossypium hirsutum* L.) (Malvaceae) flower buds (henceforth, 'squares'), making it difficult to find or observe their feeding behavior (Rosenheim et al., 2004). *Lygus hesperus* adults, on the other hand, are highly mobile and easily disturbed, making it difficult to observe their behavior for an extended period in the field. This may explain why previous

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attempts to quantify the impact of *L. hesperus* life stages on cotton square abscission have constrained insects on cotton plants or squares for a fixed period of time (e.g., Gutierrez et al., 1977; Armstrong & Camelo, 2003). In this paper we take a different approach, using laboratory and field experiments in combination with field-level correlations between *L. hesperus* density and cotton square damage at three spatial scales (individual plants, areas within fields, and whole fields) to assess relationships between *L. hesperus* developmental stage and cotton square abscission.

Lygus hesperus has been known to be an important pest of cotton for almost a century (reviewed by Leigh & Goodell, 1996). While *L. hesperus* bugs are usually present in very low densities in cotton relative to other crops such as alfalfa, they have been thought to produce large reductions in cotton yields (Leigh et al., 1988; Ellsworth, 2000). This is because *L. hesperus* adults and nymphs focus their feeding on the young developing cotton squares. When feeding on squares, *L. hesperus* injects a series of pectin-digesting salivary enzymes that cause cotton plants to abscise their squares from fruiting branches (Strong & Kruitwagen, 1968; Strong, 1970; Cline & Backus, 2002). *Lygus* damage is primarily concentrated in the anther sacs of cotton squares, and it is possible to accurately quantify anther sac damage through square dissection (Williams et al., 1987; Williams & Tugwell, 2000). Damage to anther sacs diminishes the production of growth hormones (such as auxin) that inhibit the localized concentration of abscisic acid, a prerequisite for square abscission (Strong, 1970; Addicott, 1982). Abscission in response to *Lygus* occurs primarily early in the reproductive period of a cotton plant, with subsequent squares and fruit being most susceptible to physical stresses on the plant (Stewart & Sterling, 1988, 1989).

Despite the widespread economic importance of *L. hesperus*, California growers have repeatedly stressed difficulties in predicting future damage to cotton squares even after a good estimate of *L. hesperus* density has been obtained. This unpredictable nature of *L. hesperus* damage is also reflected in scientific studies that have found both a negative impact of *L. hesperus* on cotton yields (e.g., Falcon et al., 1971; Leigh et al., 1988) and very little effect of *L. hesperus* on cotton yields (Falcon et al., 1968, 1971; Gutierrez et al., 1977). The large uncertainty surrounding the relationship between *L. hesperus* numbers and cotton square abscission has made *L. hesperus* a particularly feared pest throughout the San Joaquin Valley of California.

One potential explanation for this disconnect between *L. hesperus* densities and cotton square abscission is that different developmental stages of *L. hesperus* are behaving differently (i.e., imposing more or less damage). Past work with caged individuals and field plots has suggested that *L. hesperus* nymphs may inflict damage to squares that are equal to or perhaps greater than that of adults (Gutierrez et al., 1977; Ellsworth, 2000). In addition, recent field-based behavioral observations have suggested that *L. hesperus* nymphs spend as much time as female adults on squares and even more time than adult males spend on cotton squares (Rosenheim et al., 2004). Despite their potential as major pests, *Lygus* nymphs are very hard to sample, making them practically 'invisible' from a management perspective (Byerly et al., 1978). If nymphs generate much of the damage that occurs in cotton fields, it would be worthwhile overcoming these sampling limitations. Moreover, if *Lygus* nymphs are usually overlooked during monitoring, feeding damage caused by *Lygus* nymphs could be contributing to the unexplained variability between *Lygus* sampling and cotton square abscission.

Recent work has demonstrated that the absolute stage structure of *L. hesperus* populations is highly variable across fields (Zink & Rosenheim, 2004). In addition, season-long sampling has revealed that between-field differences in the absolute stage structure of *L. hesperus* populations are stable over the growing season, due to stage-specific predation by big-eyed bugs (AG Zink and JA Rosenheim, unpubl.) In this paper we describe a field experiment that quantifies the relative impacts of early instar *L. hesperus* nymphs, late-instar *L. hesperus* nymphs, and adult *L. hesperus* on cotton square retention. We combine this experiment with laboratory observations of feeding behavior and field correlations of cotton square damage with the densities of different *L. hesperus* developmental stages. We demonstrate that adults and late nymphal stages of *L. hesperus* are strongly correlated with cotton square damage and abscission, with a substantially weaker role for early nymphal stages.

Materials and methods

Can *Lygus hesperus* mouthparts reach preferred feeding sites in squares?

Lygus hesperus were collected from cotton fields at UC Davis and the total length of all three segments of their proboscis (not including rostrum) was measured under a dissecting microscope. We measured between 20 and 30 individuals of each nymphal stage, plus 39 adult females and 37 adult males. We then haphazardly collected cotton squares, *G. hirsutum*, cultivar Maxxa, from over 100 plants in the field, ranging from 4 to 20 mm in total length (as measured from the base of the pedicel to the tip). We sliced each square longitudinally in half and measured the distance from the square's surface to the anther sacs at three points: tip, upper (1/4 the distance from the tip to the base), and middle (half the distance from the tip to the base). Measurements were performed on 11–16 September, 2003.

Behavioral observations

We collected *L. hesperus* of each developmental stage and sex in cotton fields at UC Davis, grouping them into 2nd–3rd instar, 4th–5th instar, adult males, and adult females. Individual squares 5–15 mm long (median 8 mm) were stripped of the bracts and placed with a stem in a vertical water pic enclosed in a transparent arena. One insect was randomly assigned to the arena and placed on each square, and its behavior was directly observed every minute (feeding, resting, walking, etc.) for 4–5 h. We ran the observations for 17 2nd–3rd instar nymphs, 20 4th–5th instar nymphs, 17 male adults, and 20 female adults. We noted feeding locations on the square, recognizing four regions of the square that were defined as 90 degree quadrants (looking down on the tip of the square) around the circumference of the square. Behavioral observations were conducted on 5 August–1 September 2003.

Field cage experiment

This experiment was conducted at the West Side field station in the San Joaquin Valley, CA. Mesh cages (1 × 1 × 1 m) were laid out across two rows of cotton plants (*G. hirsutum*, cultivar Maxxa), with 12 cages to a row and with each cage separated by at least 1 m. Cages were supported with PVC pipe frames that were hammered into the soil, with mesh flaps buried with loose soil at the base to ensure complete closure. Plants were thinned to two plants per cage, with each plant on opposite sides of the cage. The mean number of nodes across all plants was 8.77 ± 0.15. Cages were randomly assigned to one of four treatments: (1) two 2nd instar *L. hesperus*, (2) two 4th instar *L. hesperus*, (3) one adult female and one adult male *L. hesperus*, and (4) no *L. hesperus* (control). Cages were arrayed in six blocks, each of which contained a single replicate of each treatment.

Before placing *L. hesperus* in the cages, cages were thoroughly searched (including soil and plants) for any insects that might eat *L. hesperus* (e.g., *Geocoris* spp.) or feed on the plant (e.g., other *Lygus* spp.). Across all 24 cages we removed 7 nymphal *L. hesperus*, 10 adult *Orius tristicolor*, four adult *Geocoris* spp., and one spider. Individuals were placed in cages 1–12 on 25 June, 2004 and cages 13–24 on 26 June. Cages were removed and plants were scored six days after the set up. Plants were mapped for retention of fruiting structures at the first and second position at every node, and then mean retention was calculated across the top five nodes. All squares were dissected to quantify the percentage of all anther sacs damaged, as an index of *L. hesperus* feeding damage that is linked with the probability of square abscission.

Field-level correlations

During the 2001, 2002, and 2003 growing seasons (late June through the first week of August) we sampled a total of 38 cotton fields throughout the San Joaquin Valley of California, USA. We sampled upland cotton fields, *G. hirsutum* (primarily cultivars Maxxa and Phytogen 72) and chose fields that had not been sprayed with insecticides in the previous three weeks. The *Lygus* adults in these fields appeared to be almost exclusively *L. hesperus* (vs. *L. elisus*), matching estimates of 96–99% *L. hesperus* from another field study (Godfrey, 2000). Previous work comparing sweep sampling with absolute sampling revealed that sweep nets accurately predict densities of every *L. hesperus* developmental stage. However, the same study showed that sweep sampling is biased toward collecting 4th–5th instar nymphs and adults, which are captured at over 10 times the rate of 1st instar nymphs (Zink & Rosenheim, 2004).

Nymphs were collected with aspirators and returned to the laboratory where their developmental stage was identified. *Lygus* nymphs are, in general, difficult to collect, making sample sizes of single *L. hesperus* instars too small to allow us to resolve their impact on square damage and retention. Therefore, for our statistical analyses we combined 1st through 3rd instars in one group and 4th through 5th instars in another group. Previous work has revealed dramatic differences between the feeding impact of early and late instar *L. hesperus* nymphs (Gutierrez et al., 1977); we chose to split nymphs between 3rd and 4th instar due to the large proportional increase in size during this developmental transition. In addition, we split our analyses into two time periods: years 2001 and 2002 were combined because both years exhibited high nymph and low adult densities. In addition, nymphs were identified to developmental stage in both 2001 and 2002. Year 2003 was analyzed separately because this year exhibited high adult and low nymph densities and because nymphs were not identified to developmental stage. In both time periods data were analyzed using multivariate regressions of plant damage vs. *L. hesperus* developmental stage.

During 2001 and 2002, *L. hesperus* adults and nymphs were collected using sweep nets across one site within a field. Samples consisted of 10 runs of 50 sweeps, with successive sweep samples taken every three to four rows, such that the area of the site sampled covered approximately 40 rows. *Lygus hesperus* nymphs were collected from sweep nets with aspirators and taken back to the lab where they were identified to developmental stage. *Lygus hesperus* adults were counted from sweep nets in the field. *Lygus hesperus*

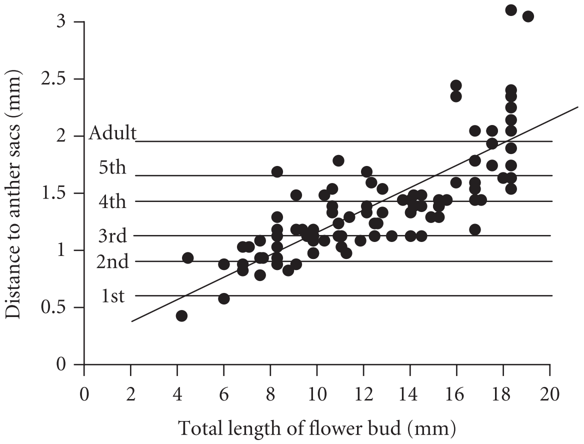

Figure 1 The average distance to anther sacs from three points on the surface of a cotton square, across squares of varying lengths (as measured from the base of pedicel to the tip). Horizontal lines represent the mean mouthpart lengths for *Lygus hesperus* of varying developmental stages measured in the laboratory.

counts were averaged, for each stage, across all samples to estimate overall numbers per field (eight fields in 2001 and nine fields in 2002). In 2003, individuals were collected and identified in the same manner, with 10 runs of 50 sweeps per field. However, we conducted these 10 runs across five separate sites located around the periphery of a large commercial cotton field (i.e., two runs per site). This allowed us to add individual fields as a blocking term in our multivariate analyses for 2003, revealing any correlations between plant damage and *L. hesperus* stage across sites within fields.

In 2001 we mapped 20 randomly selected plants from the area sampled and dissected all squares present at the first position to quantify damage to anther sacs. In 2002 we mapped 30 plants in the area sampled to quantify retention at the top five nodes. Half (15) of these plants were randomly chosen for dissection of all first position squares to quantify damage to anther sacs. The other half of these plants were tagged and revisited after 2 weeks to quantify the proportion of all first position squares retained. We used these 2002 data to correlate current anther sac damage with past square abscission (retention at top five nodes) and future (2 week) square abscission (at all nodes) across all nine fields. In 2003 we randomly collected four plants at each of the five sites per field where *L. hesperus* were sampled in order to dissect all first position squares and record square retention at the first position of the top five nodes (for a total of 20 plants mapped per field). When the majority of anther sacs were damaged, we estimated the number damaged by subtracting viable anther sacs from 100 (the approximate mean number of anther sacs in undamaged squares). All means are presented with their accompanying standard errors.

Results

Can *Lygus hesperus* mouth parts reach preferred feeding sites in squares?

The mean distance from the external surface of the square to the developing anther sacs, a preferred feeding site for *L. hesperus*, was linearly correlated with total square length ($R^2 = 0.605$, $P<0.0001$; $n = 98$; Figure 1). The mean lengths of *L. hesperus* mouthparts ranged from 0.616 mm (1st instar) to 2.004 mm (female adult). Figure 1 reveals that the smallest *L. hesperus* nymphs will not be able to feed on anther sacs of at least some squares (the larger ones), whereas the later developmental stages of *L. hesperus* are not constrained. However, the squares that are most sensitive to *L. hesperus* damage (squares < 7 mm) are accessible to essentially all stages and even the 1st instars can feed on the most sensitive 'pinhead' squares. Thus, size constraints do not rule out damaging effects from even the youngest *L. hesperus*.

Behavioral observations

Mean percent total time spent feeding on the squares varied significantly across *L. hesperus* developmental stages (ANOVA: $F_{3,70} = 3.13$, $P<0.031$; Figure 2A). Female adults spent a greater proportion of time feeding on squares relative to 2nd–3rd instars (LS means contrast: $F = 6.88$, $P = 0.011$), as did 4th–5th instars (LS means contrast: $F = 5.64$, $P = 0.020$). Male adults showed an intermediate feeding duration and were not significantly different than other stages. We also found that, for those *L. hesperus* that did feed on squares during our observations, there was a difference in the number of quadrants targeted (ANOVA: $F_{3,30} = 7.35$, $P<0.0008$; Figure 2B). Specifically, male adults fed on fewer quadrants per square relative to all other stages (LS means contrast: $F = 14.98$, $P = 0.0005$) and 4th–5th fed on more quadrants per square relative to all other stages (LS means contrast: $F = 13.88$, $P = 0.0008$).

Field cage experiment

Different *L. hesperus* developmental stages generated different levels of square abscission across the first two positions of the top five nodes across both plants (ANOVA: $F_{3,20} = 4.00$, $P = 0.022$; Figure 3). The 2nd instars were identical to controls and the 4th instars were not significantly different than controls (LS means contrast: $F = 1.98$, $P = 0.175$) or adults (LS means contrast: $F = 2.44$, $P = 0.134$), but adults had significantly higher numbers of abscised squares relative to controls (LS means contrast: $F = 8.80$, $P = 0.008$). Fourth instars were not

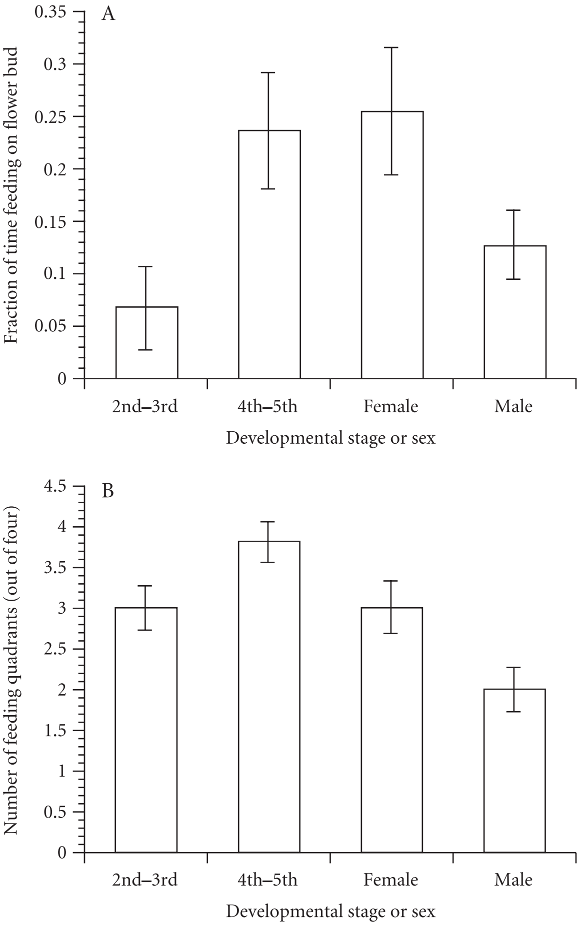

Figure 2 Laboratory observations of *Lygus hesperus* feeding behavior on cotton squares. (A) The mean proportion of time spent feeding on squares. (B) For the subset of individuals that fed on squares, the number of quadrants (out of four) that were attacked. Shown are the means ± 1 SE.

significantly different from any of the other developmental stages, but showed an intermediate level of square abscission.

Field-level correlations

For 2002 there was a positive correlation between the average number of anther sacs damaged at first-position squares, at the field level, and the percent abscission of first-position squares 2 weeks later (r = 0.94, P = 0.0001; n = 9). In addition, there was a positive correlation between the percent retention at the first position of the top five nodes (past square retention) and the proportion of first position squares that were retained over the ensuing 2-week period (r = 0.85, P = 0.004; n = 9). This suggests that current anther sac damage and past square retention are good predictors of future square retention.

Across all the 38 fields sampled in 2001–2003 there was a negative correlation between the mean anther sac damage and the mean square retention at the first position of the top five nodes (r = –0.66, P<0.0001; n = 38). We also examined correlations between *L. hesperus* stage and square damage across fields. This analysis revealed that 4th–5th instar nymphs are positively correlated with damage to anther sacs and negatively correlated with retention at the top five nodes for 2001–2002 (Table 1). Adults exhibited a similar, but marginally significant trend in 2003 (Table 2) and the densities of 1st–3rd instar nymphs were not correlated with damage or retention in any of the three years. The mean density of nymphs (individuals per 50 sweeps) was 1.70 ± 0.69 in 2001, 5.44 ± 1.81 in 2002, and 1.25 ± 0.27 in 2003. The mean density of adults (individuals per 50 sweeps) was 3.37 ± 1.17 in 2001, 3.81 ± 0.80 in 2002, and 4.00 ± 0.66 in 2003.

We also examined if adult and nymph densities are correlated with damage at the within-field level for 21 fields sampled in 2003 using multiple regression analysis. This approach controlled for differences among the fields in which sites were sampled, and confirmed that adult densities were positively correlated with anther sac damage and square abscission across sites within fields (Table 3). No such relationship was found for nymphs (Table 3). These data thus provide evidence that variation in adult *L. hesperus* density within a field is correlated with within-field variation in square damage and abscission.

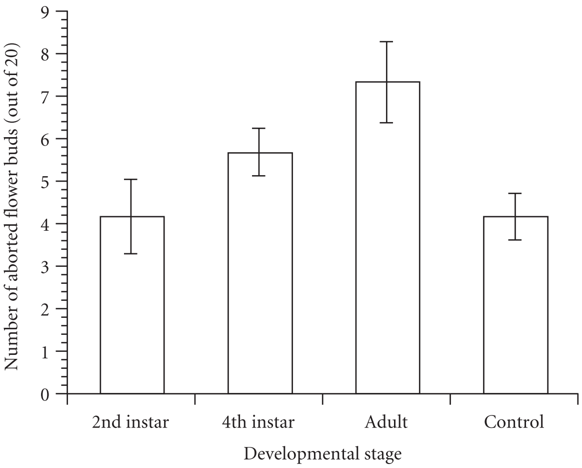

Figure 3 The number of squares abscised by *Lygus hesperus* of varying developmental stages across the first two positions of the top five nodes across both cotton plants in each cage (out of a total of 20 squares per cage). Shown are the means ± 1 SE.

Discussion

Our laboratory measurements of mouthpart length across various *L. hesperus* stages revealed that the anther sacs in

Table 1 Field-level multiple regressions relating the density of *Lygus hesperus* in different developmental stages with plant damage. Data were gathered from 17 cotton fields sampled across the years 2001 and 2002

	Percent damage to squares (anther sacs damaged)			
Factor	d.f.	Slope (SE)	F	P
Adults/sweep	1	0.442 (0.163)	0.519	0.486
1st–3rd instars	1	0.632 (1.691)	0.153	0.704
4th–5th instars	1	1.822 (0.532)	11.75	0.006

	Percent square retention (first position of top five nodes)			
Factor	d.f.	Slope (SE)	F	P
Adults/sweep	1	−0.131 (1.092)	0.014	0.907
1st–3rd instars	1	1.921 (2.885)	0.444	0.519
4th–5th instars	1	−5.192 (0.948)	30.01	0.0002

many of the squares (specifically those squares larger than 7–8 mm) are inaccessible to early instars. In addition, behavioral observations in the lab revealed that 2nd–3rd instar *L. hesperus* spend much less time feeding on squares relative to other life stages. These morphological and behavioral constraints are likely to explain the field-level correlations that revealed no role for 1st–3rd instars in square damage or abscission. In contrast, laboratory data revealed that 4th–5th instar *L. hesperus* are able to reach anther sacs across the majority of square sizes. In addition, 4th–5th instars target the most area across the surface of a square and, with female adults, they spend the most time feeding on squares. Our field-level correlations also reveal that the later developmental stages (4th and 5th instar nymphs and adults) of *L. hesperus* are likely to have a large impact on cotton square damage and abscission in certain years when nymph densities are high (years 2001 and 2002).

Table 2 Multiple regressions for 21 cotton fields sampled in 2003, relating the density of *Lygus hesperus* adults to plant damage and square retention

	Percent damage to squares (anther sacs damaged)			
Factor	d.f.	Slope (SE)	F	P
Adults/sweep	1	0.610 (0.338)	3.254	0.089
1st–3rd instars	1	1.812 (2.381)	0.579	0.457
4th–5th instars	1	−0.736 (1.341)	0.301	0.590

	Percent square retention (first position of top five nodes)			
Factor	d.f.	Slope (SE)	F	P
Adults/sweep	1	−2.452 (1.069)	5.259	0.035
1st–3rd instars	1	1.062 (7.527)	0.012	0.889
4th–5th instars	1	2.273 (4.239)	0.288	0.599

Table 3 Multiple regressions across the five sampling sites within each cotton field in 2003, relating the density of *Lygus hesperus* adults to plant damage and square retention

	Percent damage to squares (anther sacs damaged)			
Factor	d.f.	Slope (SE)	F	P
Field	20	n.a.	1.774	0.038
Adult density	1	1.223 (0.339)	12.99	0.0005
Nymph density	1	0.256 (0.529)	0.235	0.629

	Percent square retention (first position of top five nodes)			
Factor	d.f.	Slope (SE)	F	P
Field	20	n.a.	4.221	<0.0001
Adult density	1	−1.610 (0.669)	5.774	0.019
Nymph density	1	−0.826 (1.043)	0.628	0.431

Laboratory observations revealed that male adults spend less time feeding on squares relative to female adults, a result that matches previous field observations (Rosenheim et al., 2004). While *L. hesperus* sex ratio varies slightly across fields, previous work has revealed that the overall ratio of male and female adults is 1:1 (Zink & Rosenheim, 2004). In the current study, field-level correlations revealed that, for years when adult numbers are high (e.g., 2003), the density of *L. hesperus* adults is positively correlated with square damage and abscission. By sampling multiple sites within a field we were able to show that this relationship between *L. hesperus* adult density and square damage or abscission can be found across sites within cotton fields. The cage experiment also confirmed this relationship, clearly showing that adults cause significant damage and abscission of cotton squares relative to controls, with 4th–5th instars imposing an intermediate level of damage and 1st–3rd instars showing no effect on squares (as in the correlative data for all years).

Our field-level correlations from 2001 and 2002 match another study that used correlative data from experimental plots to determine that *L. hesperus* nymphs, but not adults, were negatively correlated with cotton yield (Ellsworth, 2000). However, our 2003 correlative data suggest an important role for *L. hesperus* adults in square abscission. One explanation for these differences could be that nymphs were much more abundant (and adults less abundant) in the fields sampled for 2001 and 2002, relative to 2003. This underscores the importance of our controlled cage experiment, where densities of each life stage were held constant. In addition to year-to-year variability in *L. hesperus* stage structure, it is likely that *L. hesperus* nymphs and adults are inflicting damage at different spatial scales. At the level of a field, for example, *L. hesperus* nymphs have been found to be more clustered in space relative to adults (Sevacherian & Stern, 1972). This could explain the results of Ellsworth's (2000) study if *L. hesperus* adults (but not nymphs) moved among small experimental plots that varied in insecticide applications.

Our experimental results, using large field cages, clearly point to an effect of *L. hesperus* adults with an intermediate effect of late-instar nymphs and a negligible effect of early-instar nymphs. This matches the work of Gutierrez et al. (1977) in which various *L. hesperus* stages were constrained to fruiting branches of cotton plants with mesh sleeves. While our adults were able to forage more freely relative to this study (across two whole plants), it is still possible that limiting adult movement acts to artificially inflate the role of adults in square damage. This could happen, for example, if cages concentrate feeding by *L. hesperus* adults on a few plants rather than the multiple plants over which an adult would feed over several days. However, the correlative data for multiple sites within a field suggest that *L. hesperus* adults remain in the general area in which they are creating damage. It is clear that resolving the spatial scale over which *Lygus* adults (and nymphs) both feed and disperse is critical for the design and interpretation of future studies addressing *Lygus* impact in cotton fields.

In the multiple regressions for 2003, square abscission was mostly explained by variation among fields rather than the density of adult *L. hesperus* per se. The effect of field on abscission rates may be due to intrinsic factors that were not measured, such as non-*L. hesperus* plant damage or nutrient limitation. A comprehensive understanding of the relationship between stage-dependent *L. hesperus* feeding and cotton square abscission will need to incorporate the relationship between plant state and the sensitivity to *L. hesperus* feeding. It is likely that a portion of the unexplained variation in cotton's abscission response is due to an interaction between *L. hesperus* feeding and some other, unmeasured variable(s), that vary across fields. In addition, the probability of abscission from *L. hesperus* feeding increases for cotton squares at positions further from the main stem (Armstrong & Camelo, 2003). Furthermore, abscission of an adjacent square can suppress the abscission response (Kerby & Buxton, 1981). Size of the cotton square is also a factor; smaller squares are more likely to abscise after damage (Strong, 1970).

From a management perspective, the results of this study suggest that it is important for field scouts and entomologists to pay close attention to the immature developmental stages when counting *L. hesperus* in sweep nets. Even if nymphs are accurately counted in sweep nets, however, there is an inherent bias against collecting *L. hesperus* nymphs relative to adults (Fleischer et al., 1985). In earlier work we found that sweep nets are inherently biased against collecting 1st–3rd instars but capture 4th and 5th instars at a rate that is comparable to that of *L. hesperus* adults (Zink & Rosenheim, 2004). The difficulties of collecting and counting 1st–3rd instar nymphs in a sweep net, combined with evidence that these stages do not damage the plant, mean that monitoring these life stages is only important for predicting the future presence of the more damaging later developmental stages. However, the common practice of counting only *Lygus* adults as they fly out of the sweep net will largely miss the larger nymphs in the net, nymphs such as the 4th and 5th instar that have great potential to damage cotton squares and reduce yield.

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