

Omnivore or Herbivore? Field Observations of Foraging by *Lygus hesperus* (Hemiptera: Miridae)

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ABSTRACT When important agricultural pests are omnivores instead of strict herbivores, their impact on the host plant may change as the omnivore shifts between consumption of plants and consumption of prey. *Lygus hesperus*, a key pest of cotton, is known from laboratory and field studies to be an omnivore, but no field studies have ever quantified the importance of predation as a source of food. Cotton growers have long considered the impact of *L. hesperus* on cotton to be enigmatic, because sometimes crop damage seems to be higher or lower than would be expected based upon the density of *L. hesperus* estimated through sweep net samples. Here, we conducted focal observations of *L. hesperus* foraging freely in the field to quantify the relative importance of predation versus herbivory as food resources and to determine whether omnivory was sufficiently common that it might underlie the “*Lygus* enigma.” In observations of 84 individuals over a total of 56.7 h, we did not observe any predation events. Observations conducted in the laboratory under continuous magnification also yielded no evidence of predation, suggesting that we were not failing to detect predation events on small or cryptic prey in the field. Thus, *L. hesperus* expresses predatory behavior at most very infrequently and develops essentially as an herbivore in California cotton. We did, however, find that adult male *L. hesperus* spend more of their time resting and spend less time on the vulnerable reproductive structures of the cotton plant compared with nymphal stages or adult females. Further work on the *Lygus* enigma will examine the differential ease of sampling different *L. hesperus* life stages and the possibility that they contribute unequally to crop damage.

KEY WORDS omnivory, diet selection, habitat selection, direct observations, cotton

OMNIVORY, THE HABIT OF feeding both as a herbivore and a predator, is now recognized to be widespread among insect taxa (Coll and Guershon 2002). This result has been supported by detailed food web studies (Polis 1991) and by a growing understanding of the natural history of some broadly omnivorous taxa, such as the Hemiptera (Wheeler 2001, Coll and Guershon 2002). Furthermore, theoretical work (McCann et al. 1998, Lalonde et al. 1999, Williams and Martinez 2000, van Rijn et al. 2002) and microcosm experimentation (Fagan 1997, Holyoak and Sachdev 1998) have overturned earlier predictions (May 1973, Pimm 1982) that omnivores should destabilize food webs and should therefore be rare in nature. In some agricultural ecosystems, such as cotton, many of the commonest arthropod taxa are omnivorous. This is true for many species that are generally considered to be “beneficials,” including parasitoids (Jervis et al. 1996) and predatory hemipterans (Coll 1998), lacewings (Limburg and Rosenheim 2001), and phytoseiids (McMurtry and Croft 1997), and also for some species that are generally considered to be herbivorous “pests,” such as some thrips (Trichilo and Leigh 1986, Wilson

et al. 1996, Janssen et al. 2003) and *Lygus* species (Wheeler 1976, 2001).

It is important for applied insect ecologists to understand omnivory for at least two reasons. First, when omnivores function as predators they can be important as biological control agents. This is especially true in disturbed or annual agroecosystems, where omnivores may be able to support themselves on plant-based resources and thereby maintain their populations during periods when the target pest is absent or rare (Karban et al. 1994; Walde 1995; Settle et al. 1996; McMurtry and Croft 1997; Coll 1998; Eubanks and Denno 1999, 2000; van Rijn et al. 2002). Second, when omnivores function as herbivores they can be important as crop pests. The impact of omnivore feeding on the host plant may vary as a function of the availability of arthropod prey, necessitating the use of more complex decision rules to manage their populations effectively (Alomar and Albajes 1996, Agrawal et al. 1999, Agrawal and Klein 2000; also see Reding et al. 2001, Lucas and Alomar 2002). Indeed, some omnivorous taxa may switch between functioning as important biological control agents when prey are abundant and important crop pests when prey are rare or absent (Alomar and Albajes 1996, McGregor et al. 2000).

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In this study, our focus is on the expression of omnivory by *Lygus hesperus* Knight (Hemiptera: Miridae). *L. hesperus* is a key pest of several crops in North America, including cotton, strawberries, seed alfalfa, beans, pome fruits, and some vegetables (Leigh and Goodell 1996). Although the majority of the literature describing the biology and ecology of *Lygus* spp. has focused on their role as herbivores, it has long been recognized that *Lygus* also feed as predators or scavengers of insect carrion (reviewed by Wheeler 1976, 2001). As noted by Wheeler (1976), however, few of these studies provide quantitative field data evaluating the role of *Lygus* as predators; instead, the majority of the field studies simply report casual observations of predation by *Lygus* spp. Perhaps most importantly, few studies have quantified the contribution of predation to the total diet of *Lygus*.

Producers and pest management specialists working in California cotton have for many years discussed informally an "enigma" that surrounds the management of *L. hesperus*: the relationship between the perceived density of *L. hesperus* and crop damage (abscission of flower buds, called "squares") seems to be highly variable. Some fields in which the standard sweep-net sampling produces high counts of *L. hesperus* sustain little damage, whereas other fields with much lower counts of *L. hesperus* sustain heavy damage. This enigmatic observation has never been studied scientifically, and indeed the few studies relating *L. hesperus* density to crop damage do not suggest that the enigma is real; instead *L. hesperus* density and crop damage can be strongly correlated (Leigh et al. 1988). Nevertheless, the perception of a *Lygus* enigma persists in the grower community. One goal of our study was to examine the possibility that a highly omnivorous *L. hesperus* population might be switching between plant and prey feeding, creating hard-to-predict swings in the intensity of their impact on the host plant.

A series of field studies conducted in California and Arizona created an expectation that the *L. hesperus* populations that we studied in California cotton would indeed function as omnivores. First, Eveleens et al. (1973) studied predation on *Spodoptera exigua* (Hübner) in California cotton by using outplanted egg masses. They reported that *L. hesperus* was observed several times feeding on egg masses, although it was a minor predator compared with the hemipteran predators *Geocoris pallens* Ståhl, *Orius tristicolor* (White), *Nabis americanoferus* Carayon, and the lacewing *Chrysoperla carnea* Stephens. Second, in a similar study, Bisabri-Ershadi and Ehler (1981) examined predation on *Spodoptera praefica* (Grote) eggs in California alfalfa fields and again observed *L. hesperus* attacking eggs, although they expressed uncertainty regarding how important it might be relative to what they considered to be the "major" predators *O. tristicolor*, *Geocoris* spp., and *Nabis* spp. Third, observations made during whole-plant searches of cotton plants in the San Joaquin Valley of California revealed instances of *L. hesperus* acting as a predator of a coccinellid larva, a coccinellid pupa, an egg mass of *Zelus renardii* Ko-

lenati, and an adult honey bee, *Apis mellifera* L. (J.A.R. and D. D. Limburg, unpublished data); at least for the honey bee, the *L. hesperus* was presumably acting as a scavenger. Finally, and perhaps most importantly, Hagler and Naranjo (1994) and Naranjo and Hagler (1998) concluded that *L. hesperus* in Arizona cotton was one of the top two predators of the eggs of the pink bollworm, *Pectinophora gossypiella* (Saunders), and the sweetpotato whitefly, *Bemisia tabaci* (Gennadius). Approximately one-quarter of all field-collected nymphal and adult *L. hesperus* scored positive in gut content immunoassays for having recently (<1 d) consumed one of these prey. Thus, *L. hesperus* in Arizona cotton seems to express predation on a level roughly similar to, and in some cases exceeding, other taxa that are widely recognized as important generalist predator biological control agents, including *O. tristicolor*, *Geocoris* spp., *Nabis* spp., and *Z. renardii*. Such a strong expression of omnivory by *L. hesperus* would suggest that the impact of *L. hesperus* on cotton might be modulated by the availability of arthropod prey as an alternate food resource. Such a potential for a shifting impact on the host plant would be important for *L. hesperus* management decisions.

Studies of the battery of enzymes produced by *L. hesperus* have provided further support for the view that they function as omnivores. Cohen (1996) showed that *L. hesperus* produces venom and phospholipase A₂, an enzyme that indicates an advanced state of adaptation to predation. Agusti and Cohen (2000) and Zeng and Cohen (2000, 2001) studied a long-term laboratory colony of *L. hesperus* originally derived from Arizona (A. C. Cohen, personal communication), and reported enzymatic activity profiles that were generally consistent with an omnivorous diet, although hyaluronidase activity, which is particularly characteristic of predatory taxa, was not detected.

The goal of our study was to quantify the foraging behavior, microhabitat use, and diet of *L. hesperus* foraging naturally in upland cotton, *Gossypium hirsutum* L., grown in the San Joaquin Valley of California. Because we wanted to define the range of prey consumed by *L. hesperus*, we used focal observations. Our most fundamental question was, How frequently does *L. hesperus* act as a predator of other arthropods present in cotton? To address the possibility that predation events on very small prey (e.g., eggs of spider mites or whiteflies) might be missed in some field observations, we also conducted laboratory observations of foraging by *L. hesperus* under continuous stereomicroscopic magnification.

Materials and Methods

Field Observations. Focal observations of individual *Lygus* ($N = 84$) were conducted from June through September 2001 on upland cotton in the southern San Joaquin Valley. California cotton fields can harbor both *L. hesperus* and the generally much less common *Lygus elisus* Van Duzee (Sevacherian and Stern 1972). Although the nymphal stages and adult females of

these species are difficult to distinguish definitively, male *L. hesperus* can be readily distinguished from male *L. elisus* by using a combination of the following characters: dark lines or spots on the propleuron, black pigment in the wing membrane, and the rostrum extending beyond the hind coxae (Mueller et al. 2003). Using these characters, 14 of the 14 males that we observed and collected were assigned to *L. hesperus*. We suggest, therefore, that our results apply to *L. hesperus*, although a small number of *L. elisus* also may have been observed.

Observations were made during daylight hours only. Fields, including seven commercial plantings and two smaller plantings at experimental stations, were chosen on the basis that they supported populations of *L. hesperus* and had not received pesticide applications for 3 wk before the observations. Individual *L. hesperus* were chosen for observation by walking slowly through the field inspecting all visible portions of the cotton plants for any *L. hesperus* stage. The aim was to observe equal numbers of nymphs, adult males, and adult females at each site; however, spatial and temporal variation in the age structure and sex ratio of *Lygus* populations, and in particular the difficulty of finding *L. hesperus* nymphs early in the growing season, often made this impossible to achieve.

Observers worked in teams of two and attempted to record continuously the behavior of an individual *L. hesperus* over the course of an hour. One person watched the *L. hesperus* and the other person recorded data on a hand-held computer (Psion Organizer II, Psion PLC, London, United Kingdom) operating behavioral event recording software (The Observer 3.0, Noldus Information Technology b.v., Wageningen, The Netherlands). By minimizing our movements during an observation period, we were able to avoid disturbing the focal *L. hesperus*. Although the goal was to observe individual insects for an hour, this was not always possible because some individuals were lost in flight. Continuous recordings were made of 1) the plant part on which the *L. hesperus* was present (top of leaf, bottom of leaf, petiole, stem, growing tip of plant, square, flower, and boll); 2) *L. hesperus* activity (rest, walk, and feed); 3) the identity of food items consumed or probed (including plant parts and arthropod prey); and 4) any contacts with other arthropods (natural enemies or prey). Feeding was recorded if the individual remained still with its stylets inserted into the substrate (Cline and Backus 2002). When possible, *L. hesperus* were collected after being observed to determine their nymphal stage and, for adults, their sex.

Our initial expectation was that *L. hesperus* behavior might be influenced by the plant growth stage or by the resident community of arthropods. At each site, we therefore measured the number of mainstem nodes for each of 10 plants and sampled the arthropod community by using three sampling techniques: sweep netting, leaf samples, and whole-plant visual searches. Ten sweep-net samples, each sample comprising 50 sweeps across the upper canopy of a single row of cotton with a standard 38-cm-diameter canvas

net, were conducted, and *Lygus* spp. nymphs and adults were counted in the field. A leaf sample, comprising 50 leaves collected from the fifth mainstem node from the top of the plant, was taken to quantify the densities of the dominant herbivores cotton aphid, *Aphis gossypii* Glover; spider mites, *Tetranychus* spp.; and western flower thrips, *Frankliniella occidentalis* (Pergande). The leaves were stored in 70% ethanol until they were processed in the laboratory by hand-washing them over a fine sieve (75 by 75- μ m openings) to extract the foliar arthropods. The arthropods were stored in 70% ethanol and identified and counted using a stereomicroscope. A second leaf sample comprising an additional twenty leaves taken from the fifth mainstem node was taken to quantify the density of whitefly nymphs. These leaves were kept cool and examined in the laboratory within 48 h to count and identify whitefly nymphs. To quantify the predator community, whole plant searches ($N = 10$ plants) were conducted. The plants were chosen randomly and cut below their cotyledonary scars and then carried to the edge of the field where all plant parts were inspected to count immature and adult predators.

Laboratory Observations. Laboratory observations were conducted in early October 2001 on field-collected nymphal ($N = 10$) and adult ($N = 18$) *L. hesperus* foraging on individual cotton leaves. The *L. hesperus* and cotton leaves were collected from cotton fields in the San Joaquin Valley supporting populations of whiteflies or aphids that had not received pesticide treatments in the previous 3 wk. *L. hesperus* were collected with a sweep net and stored in a cooler or refrigerator. The top five nodes of cotton plants were cut and stored with their stems in water in the laboratory. Both the insects and the plant material were used within 24 h of collection.

Individual *L. hesperus* were observed continuously under a stereomicroscope for 1 h by confining them in an arena created by affixing half of a petri dish (3.5 cm in diameter) to the undersurface of a cotton leaf with an adhesive putty (Tac 'N Stik, Elmer's Products, Columbus, OH). We placed the arenas over portions of the leaves that harbored high concentrations of potential prey for *L. hesperus* (aphids and whiteflies) and generally excluded extrafloral nectaries. The arena was mounted on a small plate that was then placed on top of a small mass of putty so that it could be tilted to provide the best lateral view of the mouthparts of the foraging bug. *L. hesperus* were allowed to acclimate to the foraging arena for 30 min before observations were begun. We used the same hardware and software as described above for the field observations to record behavioral data, but the magnified view of *Lygus* behavior allowed us to distinguish a few additional behavioral categories. Thus, we recorded *L. hesperus* activity (resting, walking, probing, grooming, and feeding) and identity of food items probed or consumed (leaf blade, leaf vein, extrafloral nectary, aphids, and whiteflies). We paid special attention to the details of the feeding behavior of the *L. hesperus*. A "contact" was recorded when the *L. hesperus* touched another arthropod. "Probing" was recorded if

Table 1. Descriptive data for cotton field sites in California's San Joaquin Valley where focal observations of *L. hesperus* were conducted

Field site (county)	Dates (2001)	No. <i>Lygus</i> observed ^a				Total observation time (h)	Cotton plant mainstem nodes ^b	Herbivore densities/leaf ^c			Predator density/plant ^d		<i>Lygus</i> density/sweep sample ^e	
		N	M	F	unk			Aphids	Whiteflies	Mites	Thrips	Nymphs	Adults	
Westside (Fresno)	23 July	1	0	0	1	0.59	18.7 ± 0.3	0.4	0	0.4	0.6	1.5	5.4	
Sheely 32 (Fresno)	24 July	0	0	0	11	3.92	17.5 ± 0.5	0.6	0	0	1.0	2.4	7.7	
Shafter 43 (Kern)	25 July	0	0	0	2	0.98	17.9 ± 0.6	0.7	0.4 ± 0.1	0.1	0.2	1.8	3.3	
Sheely 6-3 (Fresno)	2 Aug.	0	4	2	1	1.76	17.3 ± 0.4	1.5	0	0	1.8	0.2	0.3	
Sheely 8-1 (Fresno)	3 Aug.	3	3	1	0	5.03	18.7 ± 0.6	1.9	0	0	1.2	4.4	3.1	
Shafter 43 (Kern)	16 Aug.	0	0	2	1	2.60	19.5 ± 0.4	1.30	1.0 ± 0.2	0.2	0.3	1.1	1.9	
Newton 6 (Kings)	22-24 Aug.	2	6	2	2	8.59	21.5 ± 0.7	20.0	0.1 ± 0.1	0.4	1.1	2.8	7.7	
Sheely 6-4 (Fresno)	4-6 Sept.	2	2	6	0	9.77	18.0 ± 0.7	2.5	0.1 ± 0.1	0.2	0.4	0	2.0	
Jones 9 (Kings)	11-13 Sept.	7	3	2	0	9.16	24.0 ± 0.7	2.4	1.3 ± 0.4	20.7	1.7	2.5	0.6	
Jones 4 (Kings)	20-26 Sept.	9	4	5	0	14.30	22.8 ± 0.6	3.4	6.4 ± 1.0	0.2	0.3	3.8	0.6	

^a F, adult females; M, adult males; N, nymphs; unk, adults of unknown sex.

^b Mainstem node counts are means ± 1 SE for N = 20 randomly selected plants.

^c Counts of aphids, mites, and thrips (primarily *F. occidentalis*) derived from a sample of 50 leaves collected from the fifth mainstem node. Whitefly counts are for nymphal stages of sweetpotato whitefly found on 20 leaves collected from the fifth mainstem node.

^d Mean no. predators per whole cotton plant, as measured by whole plant searches (N = 10 plants searched per site).

^e Mean no. nymphal and adult *Lygus* spp. counted per sweep net sample (N = 10), each of which comprised fifty sweeps.

L. hesperus contacted a potential prey with its beak. "Feeding" was recorded if we observed the beak to pierce the substrate and stay there for >5 s. After the observation, all stages of all arthropods in the foraging arena were counted.

Data Analysis. The unit of replication for our analysis of *L. hesperus* behavior in the field was the individual bug observed; thus, each focal observation contributed a single datum to our final data set. Four observations were excluded because they were <1 min. Nonparametric Wilcoxon/Kruskal-Wallis tests were used to determine whether nymphs, adult males, and adult females differed in plant substrates used, activity budget, or feeding preferences. All summary statistics are presented as the means ± 1 SE.

Results

Field Observations. We observed *L. hesperus* (N = 84; total observation time 56.7 h) under field conditions that varied with respect to the growth stage of the plant and the densities of potential herbivore prey, *Lygus* spp., and potential predators of *Lygus* (Table 1). Contrary to our expectations, which were shaped by an extensive literature describing *Lygus* spp. as omnivores, we never observed *L. hesperus* to attack or consume any arthropod prey. Thus, our observations suggest that *L. hesperus* functions predominantly as a herbivore in California cotton and that any predatory activity that might be expressed was too infrequent to be detected by our sampling.

Although none of our field sites harbored outbreak densities of herbivores, the *Lygus* we observed did have opportunities to interact with potential prey, because our field sites supported significant populations of key cotton herbivores (Table 1). We observed *L. hesperus* to make physical contact with different arthropods (aphids, whiteflies, and thrips), but in each case these contacts seemed to occur strictly accidentally as *L. hesperus* moved across the plant surface. For example, we often observed *L. hesperus* walking while periodically touching the plant substrate with the tip of their beaks; in a few cases, *L. hesperus* engaged in this activity placed their beaks on tops of aphids. Nevertheless, this contact did not result in arrestment of *L. hesperus* or the initiation of an attack. We never observed *L. hesperus* respond to any arthropod with predatory behavior (e.g., stalking and striking); instead, the *L. hesperus* either ignored the arthropods or retreated upon contact. On two occasions we saw *Z. renardii* stalking our focal *L. hesperus*, but no attacks were recorded.

Although we did not see *L. hesperus* feed as predators, we did observe extensive feeding on plant substrates, and different stages of *L. hesperus* showed differences in feeding and other behaviors (Tables 2 and 3). Adult males spent a significantly greater proportion of their time resting than did adult females ($\chi^2 = 5.1, P = 0.02$; Table 2), but males and females both fed on a similar array of plant substrates, including vegetative and reproductive plant structures, and also

Table 2. Activity budget of *L. hesperus* observed in the field on upland cotton

	Nymphs (N = 24)	Adult males (N = 22)	Adult females (N = 20)
Rest	74.69 ± 4.27a	75.65 ± 4.52a	58.76 ± 5.58b
Walk	12.95 ± 2.21a	16.01 ± 2.68a	21.37 ± 4.34a
Feed	10.78 ± 3.95a	7.65 ± 2.66a	18.15 ± 5.07a

Data (mean ± 1 SE) represent percentages of time engaged in resting, walking, or feeding. Means within a row followed by different letters indicate significant differences ($P < 0.05$, Wilcoxon/Kruskal-Wallis test).

imbibed extrafloral nectar (Table 3). Nymphs were not observed feeding on extrafloral nectar, but otherwise they showed a pattern of feeding similar to that observed for adults. We emphasize, however, that our sampling likely underestimated nymphal feeding on squares and young bolls, because nymphs often hid under the bracts that subtended squares and bolls, making it very difficult for us to determine whether they were feeding or simply resting. Because we only recorded feeding when we could see the beak in contact with the plant substrate, we probably overestimated resting and underestimated feeding by nymphs.

Different stages of *L. hesperus* allocated their time dissimilarly to microhabitats within the cotton plant (Table 4). Adult females and especially adult males spent more time on the upper surfaces of leaves than did nymphs ($\chi^2 = 19.5$, $P < 0.0001$). Males, in particular, were often observed resting at the upwind edges of leaves in the very top of the plant canopy, with their antennae extended upward and over the edge of the leaf. We speculate that these males were sampling the wind for pheromone plumes produced by calling females. Adult females and nymphs were not observed to exhibit this distinctive behavior. Adult males also spent significantly less time on fruiting structures than did either adult females or nymphs ($\chi^2 = 12.6$, $P = 0.002$). The overall pattern of microhabitat use is consistent with the interpretation that nymphs and adult females were primarily engaged in feeding on nutri-

ent-rich plant foods (fruiting structures), whereas males were primarily engaged in searching for receptive females.

Laboratory Observations. To address the possibility that we were failing to detect *L. hesperus* predation on small or cryptic arthropod prey in the field, we observed field-collected *L. hesperus* (10 nymphs, nine adult males, and nine adult females) under continuous magnification in the laboratory for a period of 1 h. To ensure that frequent encounters would occur between *L. hesperus* and potential prey, we selected cotton leaves harboring large populations of aphids (20.1 ± 6.3 per enclosure) and whitefly eggs (194.3 ± 79.1 per enclosure). Whitefly crawlers, nymphs, and pupae were also present (6.9 ± 2.2 per enclosure).

Despite frequent contacts between *L. hesperus* and whitefly eggs, *L. hesperus* were not observed probing or feeding on any stage of whitefly. Frequent encounters also were observed between *L. hesperus* and aphids ($N = 21$). *Lygus* responded to the majority of these contacts ($16/21 = 76\%$) by retreating. The remaining five *L. hesperus*-aphid contacts comprised one case where the *L. hesperus* showed no response, one case where the *L. hesperus* touched the aphid with its beak but did not pierce it, and three cases where the *L. hesperus* probed, punctured, and killed the aphid, but then immediately retreated without feeding. Thus, in no case did we observe *L. hesperus* to consume an aphid. In two cases, we also observed *L. hesperus* to probe dead aphids and then retreat without feeding.

We did observe *L. hesperus* feeding on the cotton leaf while confined in our laboratory arenas: *L. hesperus* fed on the leaf blade and veins and took meals from the foliar extrafloral nectary. *L. hesperus* engaged in 1.8 ± 0.6 feeding bouts per hour and spent a total of 6.6 ± 2.2 min feeding per hour of observation. Thus, although *L. hesperus* did feed on the cotton leaf in the laboratory, and although we did observe some willingness to probe at least one herbivore (the cotton aphid), we again produced no evidence of consumption of prey by *L. hesperus*.

Table 3. Percentage of total feeding time allocated by *L. hesperus* to different plant substrates on upland cotton

	Nymph (N = 15)	Male (N = 12)	Female (N = 15)
Vegetative parts	61.68 ± 12.46a	48.84 ± 13.04a	45.48 ± 10.70a
Top of leaf	11.94 ± 8.20	6.31 ± 4.10	3.88 ± 3.50
Bottom of leaf	23.20 ± 10.49	4.06 ± 3.09	16.14 ± 9.22
Petiole	4.66 ± 4.01	26.96 ± 10.19	1.82 ± 1.34
Stem	7.64 ± 3.95	4.72 ± 4.72	5.37 ± 5.37
Tip of plant	10.68 ± 7.34	11.26 ± 7.71	5.39 ± 2.92
Vegetative bud	3.56 ± 3.56	5.53 ± 3.71	12.87 ± 8.18
Reproductive parts	38.36 ± 12.46a	32.14 ± 12.40a	41.32 ± 11.03a
Square	18.22 ± 9.67	19.75 ± 9.96	19.52 ± 8.94
Flower	13.43 ± 9.08	10.20 ± 8.26	15.14 ± 8.25
Boll	6.67 ± 6.67	2.19 ± 2.19	6.67 ± 6.67
Nectaries	0 a	9.01 ± 8.30ab	13.20 ± 5.42b
Foliar nectary	0	0.68 ± 0.68	3.88 ± 3.05
Circumbracteal nectary	0	8.33 ± 8.33	6.96 ± 4.65
Subbracteal nectary	0	0	2.35 ± 2.35

Means ± 1 SE within a row followed by different letters indicate significant differences ($P < 0.05$, Wilcoxon/Kruskal-Wallis test).

Table 4. Percentage of total time spent by *L. hesperus* on different plant substrates on upland cotton

	Nymph (N = 24)	Male (N = 22)	Female (N = 20)
Top of leaf	8.16 ± 2.78a	48.40 ± 7.85b	28.17 ± 6.39b
Other vegetative structures	55.20 ± 8.41a	41.81 ± 7.17a	34.44 ± 6.32a
Bottom of leaf	25.96 ± 6.33	17.44 ± 6.09	17.62 ± 5.60
Petiole	18.07 ± 5.58	9.27 ± 2.82	9.07 ± 2.91
Stem	7.52 ± 2.51	8.05 ± 4.41	4.61 ± 2.37
Tip	3.70 ± 2.54	7.05 ± 3.89	3.15 ± 1.97
Fruit	36.61 ± 9.11a	9.73 ± 3.79b	37.28 ± 8.14a
Square	11.53 ± 5.61	3.41 ± 1.75	16.68 ± 5.85
Flower	12.53 ± 6.87	0.70 ± 0.44	12.85 ± 6.99
Boll	12.58 ± 6.89	5.61 ± 3.59	7.76 ± 4.94

Means ± 1 SE within a row followed by different letters indicate significant differences ($P < 0.05$, Wilcoxon/Kruskal-Wallis test).

Discussion

We knew at the outset of our study that *L. hesperus*, like other *Lygus* spp., is an omnivore, consuming both plant-based foods and arthropod prey. Omnivory in *L. hesperus* has been documented in both the laboratory and field (reviewed by Wheeler 1976, 2001), including field studies conducted in California cotton and alfalfa (Eveleens et al. 1973, Bisabri-Ershadi and Ehler 1981). Our own informal observations made over several years of work in California cotton support this conclusion (J.A.R. and D. D. Limburg, unpublished data). What had not been established, however, was the frequency with which *L. hesperus* consume prey relative to the frequency with which they engage in herbivory. We have demonstrated in this study that *L. hesperus* in California cotton acts as a predator only very infrequently, so infrequently that we recorded zero predation events in focal observations of 84 *L. hesperus* individuals conducted over a 56.7-h period. This result does not seem to be an artifact of failing to detect predation on small, cryptic prey: laboratory observations made under continuous magnification also produced no evidence of predatory activity.

This result is important for two reasons. First, it suggests that the impact of *L. hesperus* on its cotton host plant is unlikely to be modulated strongly by the availability of arthropod prey as alternate food resources. Thus, the enigmatic observation of a highly variable relationship between the perceived density of *L. hesperus* and crop damage does not seem to be caused by *L. hesperus* omnivory. It may simply be that what seems to be the preferred prey of *L. hesperus*, eggs of Lepidoptera (Wheeler 1976, 2001) or nymphs of whiteflies (Hagler et al. 2004), are so rare in typical commercial cotton fields during the mid-season that *L. hesperus* rarely express their predatory habit. Lepidopteran eggs were sufficiently rare that they were never detected in any of our samples of cotton leaves. Whiteflies, including *B. tabaci* and the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), can be important pests in California cotton, but generally only build to high densities late in the season, when the cotton crop is no longer sensitive to *L. hesperus* damage (University of California 1996). Second, the almost strict status of *L. hesperus* as an herbivore suggests that we can manage *L. hesperus* in California

cotton simply as a potential pest, rather than as an insect that might also contribute significantly to biological control of other herbivores in the community.

Our focal observations also demonstrated something that is unremarkable but nonetheless important and as yet unrecognized in the development of sampling or management plans for *L. hesperus*: nymphs, adult males, and adult females exhibit different behaviors (Tables 2–4). Nymphs and females spend substantially more time on reproductive structures of the cotton plants (squares, flowers, and bolls), where the economically damaging feeding occurs, whereas adult males spend more time on the top of leaves, presumably searching for receptive females. This simple result, coupled with recent research on *L. hesperus* in Arizona cotton reported by Ellsworth (2000) and Ellsworth and Barkley (2003), suggesting that nymphal stages may be particularly important in generating crop damage, has refocused our attempts to explain the *Lygus* enigma on the role of *L. hesperus* stage-specific behavior.

Reconciling Studies on *L. hesperus* Feeding Biology. How can we reconcile our primary result that *L. hesperus* functions almost exclusively as an herbivore with previous reports by Hagler and Naranjo (1994) and Naranjo and Hagler (1998) that *L. hesperus* is a major predator of pink bollworm and sweetpotato whitefly eggs, on a par with the important biological control agents *O. tricolor*, *Geocoris* spp., and *Nabis* spp.? Although Arizona and California populations of *L. hesperus* have access to different suites of potential prey, Arizona *L. hesperus* have been shown to be major predators of sweetpotato whitefly eggs (Hagler and Naranjo 1994, Naranjo and Hagler 1998) and nymphs (Hagler et al. 2004), whereas California *L. hesperus* given access to the same stages of sweetpotato whitefly in both the field and the laboratory did not express any predatory behavior. We will address five nonmutually exclusive possibilities for these divergent observations, beginning with the one that we think is most likely.

First, it is possible that Arizona and California *L. hesperus* are fundamentally similar, and express different amounts of predatory behavior because they are foraging in environments that differ substantially in the density of suitable prey. The pink bollworm is

not established in California's San Joaquin Valley (University of California 1996), and thus this major prey item is absent; as discussed above, other eggs of Lepidoptera are generally only found in California at low densities. Although whiteflies are often present in mid-season cotton, and they were present at our study sites, they generally do not reach high densities until the late summer or fall, after the cotton crop is no longer sensitive to damage by *L. hesperus*. The fields that we sampled never harbored high densities of whitefly nymphs (Table 1). Although our laboratory trials did use higher densities of whitefly eggs and nymphs (nearly 200 eggs and seven nymphs on average per 3.5-cm-diameter circular enclosure), these densities are still very low compared with those used in the laboratory studies reported by Hagler et al. (2004) (837 eggs, 704 nymphs, and 43 adults on average per 3.5-cm-diameter circular enclosure). To provide a preliminary evaluation of whether California *L. hesperus* would express levels of predation typical of Arizona populations, we sent *L. hesperus* collected in Fresno County during September 2003 to James R. Hagler, who tested them using the same assay procedures and similarly high whitefly densities (764 eggs, 279 nymphs, and 50 adults on average per 3.5-cm-diameter circular arena) as reported in Hagler et al. (2004). Four California *L. hesperus* were observed for a total of 2 h, yielding a total of 60 plant feeding events and eight predation events (six on nymphs and two on adults; J. R. Hagler, personal communication). These predation rates are very similar to those reported in Hagler et al. (2004) (e.g., they report an average of 2.4 nymphs preyed upon per hour). Although preliminary in nature, these observations are consistent with the interpretation that California and Arizona populations of *L. hesperus* have similar underlying potentials to act as predators, with Arizona populations expressing this potential more often because of their much more frequent encounters with prey.

Second, it is possible that intraspecific genetic variation exists for the expression of omnivory by *L. hesperus*. That is, Arizona populations may be closer to the "predator end" of the omnivory spectrum and California (San Joaquin Valley) populations may be closer to the "herbivore end." Although we are aware of no studies specifically quantifying intraspecific genetic variation in the expression of predation by omnivores, genetic variation in food resource use is certainly widespread in insect taxa (Futuyma and Peterson 1985). However, the preliminary data just discussed (J. R. Hagler, personal communication) are not consistent with the hypothesis that California *L. hesperus* populations are fundamentally restricted to an herbivorous lifestyle. A side by side comparison of Arizona-derived and California-derived *L. hesperus* populations in a controlled experimental setting would offer the most definitive means of testing this hypothesis.

A third hypothesis to explain the apparent discrepancy between our results and those of Hagler and Naranjo (1994) and Naranjo and Hagler (1998) concerns a limitation of our study: our observations were

conducted during daylight hours only. Given that *Lygus* spp. are active both during the day and night, might *L. hesperus* be acting as a predator primarily (or exclusively) at night? This "Dr. Jekyll and Mr. Hyde" hypothesis seemed to receive support in a recent study of *Lygus lineolaris* (Palisot de Beauvois) by Pfannenstiel and Yeorgan (2002). These authors reported that *L. lineolaris* and other "minor" predators of *Helicoverpa zea* (Boddie) eggs in soybean and corn were active as predators only nocturnally. However, they present data for these minor predators treated as a group, and when the data for *L. lineolaris* are viewed in isolation there is no trend toward nocturnal predation: approximately equal sampling intensity during the day and night revealed eight predation events during the day and six during the night (R. S. Pfannenstiel, personal communication). Furthermore, previous field studies of *L. hesperus* have documented predation during daylight hours (Eveleens et al. 1973; Bisabri-Ershadi and Ehler 1981; J.A.R. and D. D. Limburg, unpublished data), and we are unaware of any omnivores that shift between predation and herbivory on a diel cycle. Thus, current evidence supports the interpretation that California *L. hesperus* act as predators only infrequently, but not only at night.

A fourth possibility is that our observations of *L. hesperus* were problematical in other ways. They may have been too short or too intrusive to document predation adequately. Although we cannot rule out this possibility, it seems unlikely given our success in quantifying predation and herbivory by other omnivorous predators in cotton, including *O. tristicolor*, *Geocoris* spp., *Nabis* spp., and *Z. renardii*, by using the same techniques that we used here (Cisneros and Rosenheim 1998; Rosenheim et al. 1999; J.A.R. and D. D. Limburg, unpublished data). Focal observations revealed 33 predation events by *O. tristicolor* (over 69.4-h total observation time), 24 predation events by *Geocoris* spp. (over 75.1 h), 18 predation events by *Nabis* spp. (over 66.0 h), and 34 predation events by *Z. renardii* (over 78.3 h) (J.A.R. and D. D. Limburg, unpublished data). We emphasize that Hagler and Naranjo (1994) and Naranjo and Hagler (1998) concluded that predation by *L. hesperus* was on a par with exactly these hemipterans in their Arizona cotton fields. Clearly, populations of *L. hesperus* in California cotton do not exhibit predation to the same extent as these other hemipterans.

Finally, given that it is enzyme-linked immunosorbent assay-based gut assays of *L. hesperus* that have suggested a major predatory role for a *Lygus* species in Arizona cotton fields, it is possible that any of the various interpretational problems associated with this method of quantifying predation may be operating (reviewed by Hagler et al. 1992, Naranjo and Hagler 1998). Nevertheless, Arizona populations of *L. hesperus* show high levels of predatory activity in petri dish assays when confined with sweetpotato whitefly nymphs (Hagler et al. 2004), and as discussed above, preliminary data for *L. hesperus* collected from California cotton suggest that they express a similar level of predation when given access to the extremely high

whitefly densities that characterize some Arizona cotton fields (J. Hagler, personal communication). Thus, *L. hesperus* may express an almost purely herbivorous feeding habit in California cotton simply because they rarely encounter highly preferred prey (e.g., lepidopteran eggs) and require extremely high encounter rates with less preferred prey (e.g., whitefly nymphs) before they will act frequently as predators.

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