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Spider predators of lepidopteran eggs in south Texas field crops

Robert S. Pfannenstiel *

USDA-ARS, 2413 E. Hwy 83, Weslaco, TX 78596, USA

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Abstract

Observations were made of spiders attacking lepidopteran eggs in south Texas field crops (cotton, corn, and soybean) from 2001 to 2004. Twelve species of spider from seven families were observed feeding on the eggs during the 4 years. These spiders were primarily cursorial hunting spiders, and they were observed feeding on eggs most frequently in cotton, representing 26.6% of all observations in cotton over the 4 years. Spider predation on eggs was proportionally less frequent in corn and soybean with 6.3% and 15.4% of observed predation in those crops, respectively. Four species of spider were responsible for 86.1% of the predation by spiders. The anyphaenid *Hibana futilis* (Banks) was the spider most frequently observed feeding on lepidopteran eggs during the 4 years of this study, constituting 45.1% of all spiders observed. *Grammonota texana* Banks (Linyphiidae), *Hibana arunda* Platnick (Anyphaenidae), and *Cheiracanthium inclusum* (Hentz) (Miturgidae) were the 2nd, 3rd, and 4th most frequently observed spiders constituting 15.6%, 12.8%, and 11.7% of all spiders observed, respectively. Most spiders represented taxa that are known to forage without a web. However, *G. texana* was observed feeding on eggs independent of a web, which is uncharacteristic of linyphiids. Other cursorial hunting spiders feeding on eggs included members of the Clubionidae, Corrinnidae, and Salticidae. Ninety-eight percent of all observations of egg predation by spiders were nocturnal; only the Salticidae were diurnal. It is likely that previous studies of predation in crops have vastly underestimated the importance of spiders as predators of lepidopteran eggs due to inadequate evaluation of nocturnal predation.
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Keywords: Nocturnal; Cursorial spiders; Egg predation

1. Introduction

Spiders have been reported to feed on lepidopteran eggs in the field (review by Nyffeler et al., 1990; Ruberson and Greenstone, 1998; Pfannenstiel and Yeargan, 2002); however, in many cases these reports were anecdotal, and, with the exception of the more recent studies, there was little reason to suspect that spiders might be important predators of the egg stage of lepidopteran pests in agricultural settings.

Despite the frequency of anecdotal observations, there are few data on the propensity for most spiders to accept eggs as prey, or quantifying egg predation by spiders in either natural or agricultural settings. Sessile pests such as scale insects and sessile life stages such as eggs are believed to be less vulnerable to predation by spiders than motile stages. Recently, however, evidence has been accumulating that certain spider taxa may frequently prey on lepidopteran eggs. Studies in cotton using radioactive markers (McDaniel and Sterling, 1979, 1982) indicated that spiders may have been feeding on eggs. Nevertheless, these data were not definitive because the markers could have been acquired through intraguild predation. Using a more definitive antibody-based technique, Ruberson and Greenstone (1998) found that the winter spider *Cheiracanthium inclusum* (Hentz) (Miturgidae) was a frequent predator of eggs. *C. inclusum* has also been reported feeding on eggs in cotton (McDaniel and Sterling, 1982) and in apple orchards (Miliczky and Calkins, 2002). The clubionid *Clubiona abbottii* Gertsch has been observed feeding on eggs relatively commonly in soybean and corn (Pfannenstiel and Yeargan, 2002).

* Fax: +1 956 969 4888.
E-mail address: rpfannenstiel@weslaco.ars.usda.gov

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Lepidopteran pests of field crops are subject to significant mortality from predation and often do not attain pest status unless the natural enemy complex is reduced through the application of pesticides. Unfortunately, there have been few studies to document predation on eggs in the field that specifically addressed nocturnal events [with the exception of Pfannenstiel and Yeargan, 2002; Pfannenstiel, 2005]. Also, many previous studies on egg predation in the field may suffer from bias due to unequal sampling of predator groups or potential contamination due to intraguild predation on other predators that might contain prey markers, particularly in studies using radioactive labeling of eggs. When nocturnal predation has been characterized, invariably there are taxa identified that were not recognized as contributing significantly to mortality (Pfannenstiel, 2005). The contribution of spiders, which are predominantly nocturnal, may be underrepresented in many studies due to their cryptic activity patterns and therefore may play a greater role here than previously recognized. In south Texas, spiders were the most frequently observed predators of lepidopteran eggs in cotton (Pfannenstiel, 2004, 2005).

To address the gaps in our knowledge of the predators causing mortality of lepidopteran eggs in south Texas field crops, I conducted several studies in the Lower Rio Grande Valley of Texas from 2001 to 2004 to evaluate egg predation on two common lepidopteran pests. Spiders committed an unexpectedly large percentage of the predation events that were observed. This report summarizes the observations of spiders feeding on lepidopteran eggs found in cotton, corn, and soybean.

2. Materials and methods

This report summarizes data on spider predation on eggs of *Helicoverpa zea* (Boddie) and *Spodoptera exigua* Hübner (both Lepidoptera: Noctuidae) from several studies using similar techniques to address the effects of crop type, egg type, and crop diversity on predation rates and predator complexes in south Texas. Cotton, corn, and soybean plots or fields were established using commonly accepted production practices with 1-m row spacing. Most plantings were watered with drip irrigation; however, some cotton plots were flood-irrigated in 2003. Crops were planted between 15, February and the 30, March in each year. Only one pesticide application was made during the 4 years of study, comprising a single application of Lannate (methomyl) in the very early spring of 2002 against a severe thrips infestation in seedling cotton. Predation was not evaluated in this plot until 47 days post-treatment. A 3-m buffer of bare ground separated all plots.

Deployment of eggs and observation techniques were as described by Pfannenstiel and Yeargan (2002) and slightly modified in Pfannenstiel (2004). In studies conducted only in cotton, sentinel egg masses (*S. exigua*) or egg groups (*H. zea*, 10 eggs per sheet—described below) were placed in the field and then monitored at 3-h intervals for the next 24 h. In studies involving cotton, corn, and soybean plots only sentinel *H. zea* eggs were used. *H. zea* and *S. exigua* colonies were maintained in the laboratory by modified methods of Ignoffo (1965). Adults were placed in 3.8 L ice cream cartons lined with green florist paper for oviposition; a 10% sucrose solution was provided as a food source. Florist paper on which eggs had been deposited were collected daily; paper on which eggs had been laid was cut into small (3–20 cm^2) sections ("egg sheets") containing either 10 *H. zea* eggs or one *S. exigua* egg mass each. Egg groups or masses were then placed in a refrigerator at 4 °C to stop development until used or discarded after 4 d. Groups of 10 *H. zea* eggs (as opposed to 1 egg) were used to extend the amount of time that a predator feeds, thus increasing the probability of observing predation events. All eggs in each *S. exigua* egg mass (range 20 to ~160 eggs/mass) were counted and recorded before placement into the cotton field.

Eggs were transported to the field in an ice chest with cold packs and then attached to plants at 1500 h by stapling the egg sheets in the upper canopy. Afternoon was used for deployment of eggs for purely logistical purposes. *H. zea* eggs typically take 2.5 or more days to develop in the field in Texas and would be available to predators throughout this time (personal observation). Paper sections containing eggs were not used if any of the eggs were dislodged during transportation. In cotton and soybean, egg sheets were attached in the upper part of the canopy at about 50–80% of plant height and this relative location was maintained as the plants developed. In corn, the egg sheet was attached to one of the small leaves (husk terminals) directly adjacent to the silks on the primary ear of a corn plant or if in pre-reproductive corn at the base of a true leaf. Lepidopteran pests of field crops such as cotton often deposit their eggs on the foliage of the middle to upper parts of the plant (Terry et al., 1987; Sappington et al., 2001) although often on the undersides of leaves. Placing the eggs on the top of leaves was done to facilitate observation. Neussly and Sterling (1994) found no differences in predation on *H. zea* eggs between the upper and lower leaf surfaces in cotton in central Texas, and this pattern was corroborated in this study (unpublished data).

Egg groups were observed at consecutive 3-h intervals from 1800 h onward CDT for the following 24 h. This distribution of sampling times results in 4 daytime samples (0900, 1200, 1500, and 1800 h) and 4 nighttime samples (2100, 2400, 0300, and 0600 h). Sunrise occurred just as the 0600 h sample was being completed, and sunset occurred just prior to initiation of the 2100 h sample, allowing for equal numbers of day and night samples despite a photophase of about 14 h. Individual egg sheets were replaced whenever all eggs on a sheet had been consumed. All spiders observed feeding were collected and reared to adulthood in the laboratory on a diet of *H. zea* eggs to facilitate identification. Adult spiders that could not be identified by the author were sent to an expert on Texas spiders for identification (Allen Dean, Texas A&M University).

Overnight trials were conducted on 8–12 dates between the months of April and August in each year from 2001 to 2004. A total of 200–350 sites with sentinel eggs were observed on any one date. Because the data summarized here comes from several studies, the distribution of data varies. Cotton was included in all of the studies that were used to collect the data presented here. Corn and soybean were included in half of the studies and these were conducted over a shorter time frame due to their shorter growing season.

Observations of spider predation on lepidopteran eggs in south Texas are summarized here with the primary goal of characterizing the egg-feeding spider community. Additionally, I compared the frequency of spider predation in cotton, soybean, and corn, the frequency of spider predation on *H. zea* and *S. exigua* eggs in cotton, and characterized the diel periodicity of spider predation by species or other suitable taxa. To determine if there was an effect of year on observations of predation by crop or by egg type, statistical comparisons on observations of predation by year for these data were conducted using the *G* test of Independence (Sokal and Rohlf, 1994) when the sample size was sufficient. If the analysis showed no significant effect of year, or if there was insufficient sample size to test for a year effect, then the data from all years was pooled and the main effects (crop) tested with the *G* test for Goodness of Fit (McDonald, 2007–2008). All pair-wise tests of differences among cotton and soybean and in predation on the two egg types were analyzed using the Exact Binomial Goodness of Fit Test (McDonald, 2007–2008) against the *a priori* hypothesis that no differences in spider observations would exist between either crop or egg type. It should be noted that this test provides a *P* value but no explicit test statistic.

3. Results

Out of 1565 total observations of predation, 23.4% was committed by spiders. A total of 366 spiders were observed feeding on eggs over the 4 years (77, 123, 83, and 83 in 2001–2004, respectively) Many other arthropods were also observed preying on eggs (Pfannenstiel, 2004, 2005) including the red-imported fire ant *Solenopsis invicta* (Buren) (Hymenoptera: Formicidae) and several *Geocoris* spp. (Hemiptera: Geocoridae), however these were not germaine to the observations of spider predation on lepidopteran eggs and will not be reported here. Spider egg predators were dominated by a guild of cursorial hunting spiders comprised primarily of four species in the Anyphaenidae, Miturgidae, and Linyphiidae (Table 1) that were responsible for 86.1% of the spiders observed feeding on eggs. Other spider families were observed preying upon eggs, including the Clubionidae, Corrinidae, Salticidae, and Dictynidae, but these were relatively infrequent. Of the four most common spider species, both adult and immature stages were observed to prey upon eggs. Spider predation was first observed in late April or May of each year and the frequency of observations generally increased as the summer progressed. In August, all stages of spiders were present in cotton fields, suggesting complete overlap of generations by this time.

Table 1
Spiders observed feeding on eggs in south Texas field crops from 2001 to 2004

Spider	Frequency observed	Percent
Anyphaenidae		
Hibana futilis (Banks)	165	45.1
Hibana arunda Platnick	47	12.8
Lyniphiidae		
Grammonota texana (Banks)	57	15.6
Miturgidae		
Cheiracanthium inclusum (Hentz)	43	11.7
Clubionidae		
Clubiona kiowa Gertsch	11	3.0
Clubiona maritima L. Koch	3	0.8
Salticidae		
Hentzia palmarum (Hentz)	4	1.1
Others/unidentified	5	1.4
Dictynidae		
Phantyna segregata (Gertsch & Mulaik)	3	0.8
Dictyna bellans Chamberlin	2	0.5
Emblyna sp.	2	0.5
Corinnidae		
Meriola decepta Banks	4	1.1
Trachelus volutus Gertsch	1	0.3
Unidentified/Escaped/Died	19	5.2
Total	366	

Observations are pooled from all crops.

Of the egg predation events observed, 26.6% in cotton, 15.4% in soybean, and 6.3% in corn were by spiders. When considering only those studies where the frequency of observed predation events can be directly compared among the crops, there were twice as many observations of spiders preying on eggs in cotton than in corn or soybean which is significant at the $\alpha = 0.1$ level ($G = 5.08$; $df = 2$; $P = 0.079$) (Fig. 1a). When spider predation in cotton is compared to just soybean over its longer growing season (than corn), there was no effect of year on the pattern of predation ($G = 0.926$, $df = 3$, $P = 0.819$), however the difference in observations by crop were more significant ($P < 0.0001$) (Fig. 1b). The association of observations of the four most frequently observed spiders with cotton and soybean is consistently biased towards cotton although there were only large enough sample sizes to analyze *Hibana futilis* and *G. texana* (Fig. 2).

The cursorial hunting spider *H. futilis* (Banks) (Anyphaenidae) was the spider most frequently observed preying upon eggs in three of the 4 years (2001–2003) and the second most common in 2004, constituting 45.1% of all spiders observed feeding on eggs (Table 1, Fig. 3). *Hibana arunda* Platnick was the second most frequently observed in 2001 and 2002 and was the third most frequently

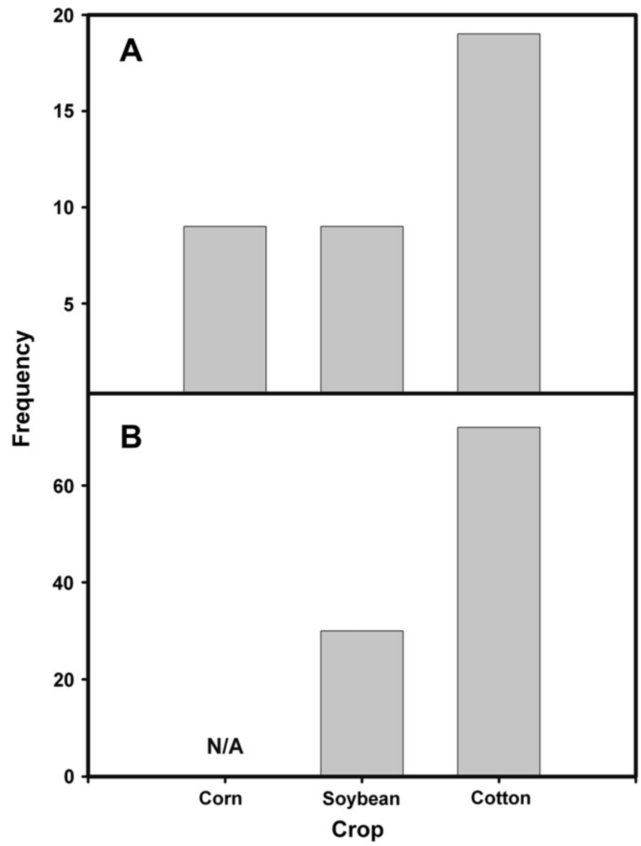

Fig. 1. Observations of spider predation summarized from dates where there were equal numbers of sample sites in (A) corn, soybean, and cotton and (B) soybean and cotton.

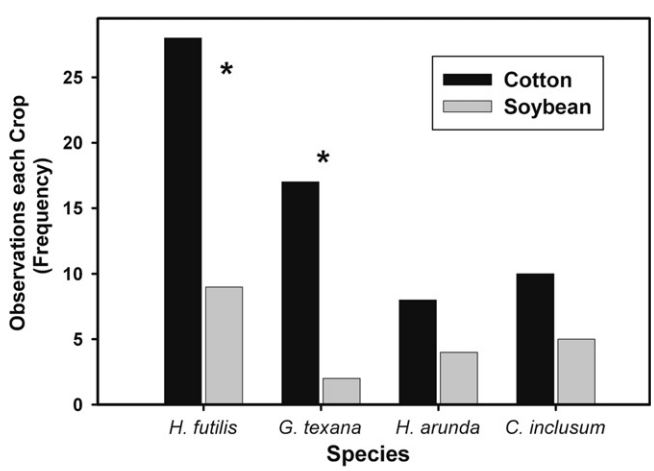

Fig. 2. Comparative predation of lepidopteran eggs by the four most commonly observed spiders in cotton vs. soybean. Where sample sizes were sufficient ($n \geqslant 20$) statistical comparisons were made by the Exact Binomial Goodness of Fit Test. All tests with sufficient sample sizes were significant at $P \leqslant 0.001$ and are indicated by an $*$.

observed spider overall (12.8% of all observations). However, neither *Hibana* species has been previously mentioned in the literature as a predator of insect eggs.

Grammonota texana (Linyphiidae) was the second most frequently observed spider feeding on eggs. However, this spider had been rare in 2001 and 2002, accounting for less than 1% of observations before becoming the most frequently observed spider in 2004 (Fig. 3). Whereas most species of Linyphiidae typically forage using webs (Kaston, 1972), none of the observations of *G. texana* feeding were in association with a web. In laboratory containers, *G. texana* did construct a rudimentary space web, but it is not known what proportion of time it allocates to active foraging vs. foraging with a web.

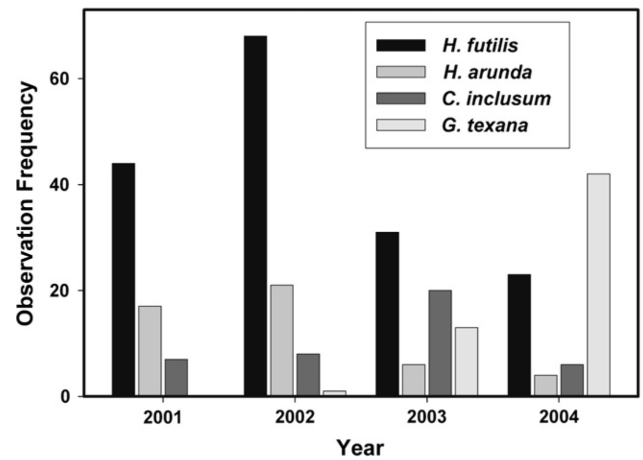

Fig. 3. Observations of the four most frequently observed spiders from 2001 to 2004.

Another wandering spider, *C. inclusum* (Miturgidae), was the fourth most common spider observed feeding on eggs overall and the second most frequently observed in 2003 (Fig. 3). *C. inclusum* is widely distributed in North America and has been implicated as a potentially important predator of lepidopteran eggs in other studies of egg predation in cotton (McDaniel and Sterling, 1982; Ruberson and Greenstone, 1998) and apples (Miliczky and Calkins, 2002). Several of the other spider taxa observed feeding on eggs have natural histories similar to the anyphaenids including the Clubionidae and the Corrinnidae. *Clubiona kiowa* Gertsch was observed feeding on eggs in all years.

Almost all observations of feeding by spiders were nocturnal (Fig. 4). Only the Salticidae were day-active with all nine individuals observed feeding on eggs between noon and sunset. Of the nocturnally active spiders, *H. futilis*, *H. arunda,* and *C. inclusum* were active primarily from 2100 h to 0300 h while the activity of *G. texana* increased later in the scotophase peaking from 0300 to 0600 h (Fig. 4).

In a study conducted in cotton alone, I compared predation on *H. zea* and *S. exigua* eggs. Only the sum of total observations of spiders preying on each egg type had consistently enough samples sizes to test for an effect of year; and no significant effect of year was found ($G = 3.70$, $df = 3$, $P = 0.296$). Therefore, observations of predation for each spider species were pooled across the 4-year observation period for further analysis. Of the individual spider species, only *H. futilis* and *G. texana* had sample sizes large

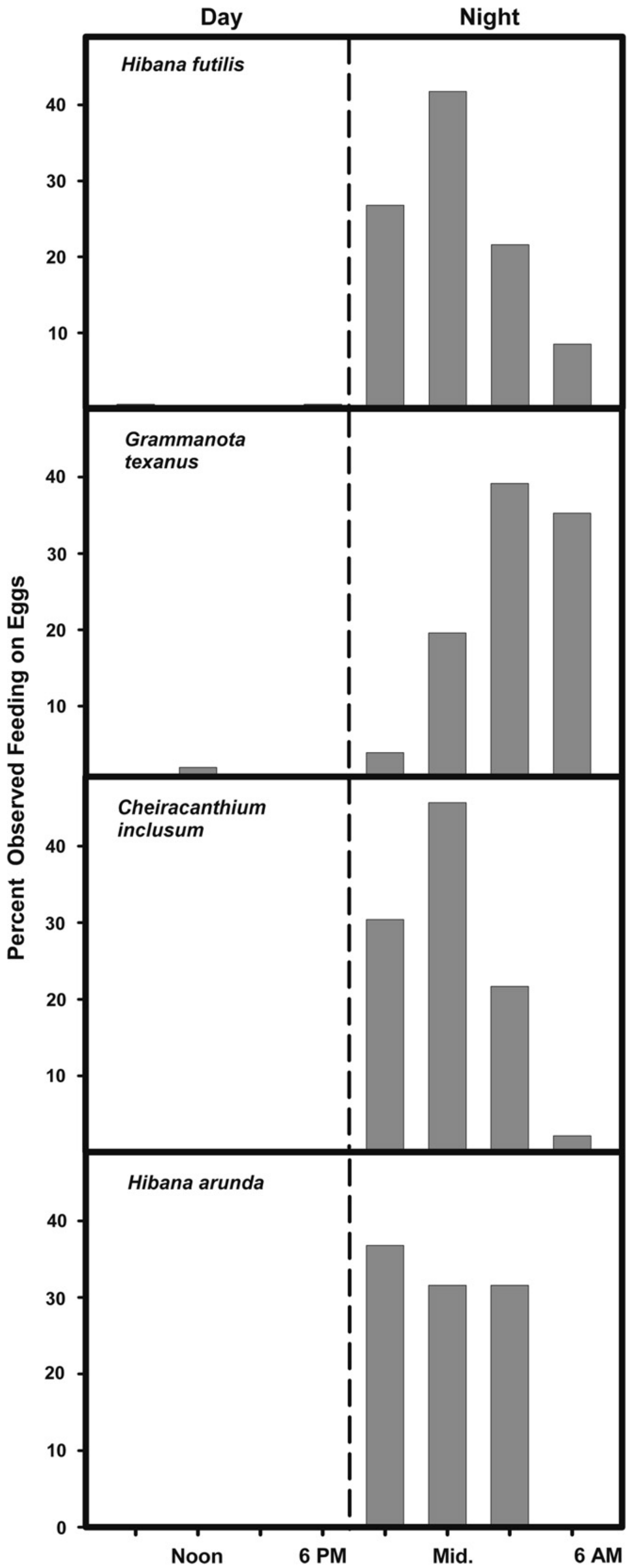

Fig. 4. Diel periodicity of observations of spiders feeding on eggs. Frequencies for each sampling period were converted to the percentage of all observations of that species feeding during that time.

enough to test even when pooled; in both of these species there were significantly more observations of predation on *H. zea* than on *S. exigua* eggs (Fig. 5). *H. arunda* was

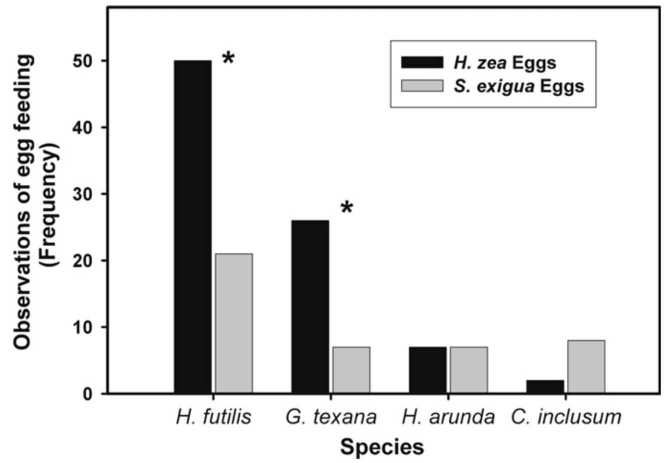

Fig. 5. Observations of feeding by cursorial spiders on *H. zea* and *S. exigua* eggs in cotton. Where sample sizes were sufficient ($n \geqslant 20$) statistical comparisons were made by the Exact Binomial Goodness of Fit Test. All tests with sufficient sample sizes were significant at $P \leqslant 0.001$ and are indicated by an $*$.

not observed feeding often enough in this study to evaluate predation, however in this case feeding on the two egg types was equal. Similarly, there were not enough observations of *C. inclusum* to analyze statistically, however this was the one species observed feeding on *S. exigua* more frequently than on *H. zea* in this study.

4. Discussion

Most observations of spiders feeding on eggs have been anecdotal, the results of studies using indirect methods, or made under laboratory no-choice conditions. Laboratory studies using no-choice tests on egg feeding by spiders, such as those conducted by Miliczky and Calkins (2002), and Pearce et al. (2004), suggest potential efficacy, but field studies are necessary to ensure that feeding observations are not artifacts of confinement. These are the first detailed field studies to document that spiders may act as important predators of the egg stage of lepidopteran pests. In the case of cotton, the spiders were particularly important and comprised 26.6% of all observations of egg predation during the 4 years. Little is known about the ecology or behavior of most of the spiders observed feeding on eggs during this study. Three of the most frequently observed species (*H. futilis*, *H. arunda,* and *G. texana*) have no references outside of the taxonomic literature and checklists of occurrence in different localities. However, there is building evidence that *Hibana* species may be important predators in agricultural systems. Recently, *H. velox* has been reported as an important predator in Florida citrus (Amalin et al., 2001), and *H. incursa* has been recently implicated as a predator in pecans and cotton in New Mexico (Richman, 2003). The only spider commonly observed in south Texas that has been previously studied is *C. inclusum*. This species has been implicated as a predator of lepidopteran eggs in cotton (McDaniel and Sterling, 1982; Ruberson and Greenstone, 1998), soybean (Buschman et al., 1977; Richman et al., 1980) and of leafminer larvae (Amalin et al., 2001) and psyllid nymphs (Michaud, 2004) in Florida. Its congener; *C. mildei* has also been reported as an important predator of lepidoptera (including eggs) in tree fruits (Mansour et al., 1980; Miliczky and Calkins, 2002). *Grammonota texana* and *C. kiowa* have not been reported in the literature as potentially important predators. The clubionid *C. abbottii* L. Koch has been observed feeding on lepidopteran eggs in soybean and corn in Kentucky (Pfannenstiel and Yeargan, 2002) and in Louisiana sugarcane (Negm and Hensley, 1969). Despite the anecdotal aspect of most observations of egg predation by spiders, these studies suggests that egg predation is quite common by certain spider taxa and these spiders play an active and important role as part of the predator complexes reducing lepidopteran populations in field crops.

Spiders made up a relatively larger proportion of the predators observed in cotton (26.6%) than in soybean (15.4%) or corn (6.3%). All four of the more common spider species were more frequently observed feeding on eggs in cotton than in soybean. These cursorial spiders have been demonstrated to actively feed on extrafloral nectaries in cotton (Taylor and Pfannenstiel, in press) and the abundance of these nectar sources may lead to improved spider survival, development, and fecundity (Taylor, 2004, Taylor and Pfannenstiel unpublished data). The abundance of nectar sources in cotton may lead to higher densities and increased impact of cursorial spiders than is observed in crops without nectar sources (soybean and corn).

During these studies, intraguild predation was observed on several occasions. When cursorial spider densities are high, intraguild predation might significantly affect the complex of predators present in the crop. This would most likely be to the detriment of juveniles or the smaller spider species such as *C. kiowa*. *H. arunda* adults are the largest cursorial spiders in this system, with *C. inclusum* adults close in size. *H. futilis*, which was the dominant species numerically, were observed as prey of *H. arunda* on several occasions.

Most of the spiders observed feeding on eggs were cursorial hunting spiders but there were two notable exceptions; *G. texana* and several dictynids. *Grammonota texana* was frequently observed feeding on eggs in 2003 and 2004. This species builds a very rudimentary web when observed in the laboratory and likely spends a portion of its time actively foraging. None of the observed predation events by this spider were associated with a web of any kind. The observations of dictynids feeding on eggs occurred when an individual constructed a web above an egg sheet.

Few spiders were observed feeding on eggs during the day; almost all of the predation by spiders occurred at night. The only spiders primarily observed during the day were the Salticidae, which appear to be primarily diurnal foragers. All of the other spiders observed were primarily nocturnal.

Egg type did significantly affect the likelihood of observing predation with approximately twice as many observations of predation by *H. futilis* and *G. texana* on *H. zea* as on *S. exigua* eggs. This was unexpected because there was some thought that predation would be more easily observed on the larger *S. exigua* egg masses. Both of these species are relatively smaller than *H. arunda* and *C. inclusum* and would be less likely to consume all of the eggs in a short time, particularly in a *S. exigua* egg mass. It is possible that the *S. exigua* eggs are less palatable; in a laboratory study, *H. futilis* developed more slowly, had lower survival rates and lower fecundity when reared on *S. exigua* eggs in comparison to *H. zea* eggs (unpublished data). Information on the ecology and biology of many of these species is sorely lacking, we know virtually nothing of their prey range.

It is likely that the cursorial spiders are an important source of mortality for numerous pests in field crops such as cotton, and possibly in many other crop systems as well. During the period when these studies were conducted, egg mortality (24 h) ranged from 25% to near 100% and spiders were among the most important predators in all three crops (Pfannenstiel, 2005). Although this study has focused on the predation of lepidopteran eggs, spiders preyed on other pests including various lepidopteran larvae and the cotton fleahopper, *Pseudomatoscelis seriatus* (Reuter) (Hemiptera: Miridae). These spiders are very active searchers and can cover large areas of crop canopy while foraging (personal observation). Additionally, several of these wandering spiders can consume many eggs on a daily basis [>200 *H. zea* eggs/day for adult female *H. arunda*, *H. futilis*, and *C. inclusum* (unpublished data)] suggesting that they could not only consume many single eggs (e.g., *H. zea*) but also entire egg masses of those lepidopterans that deposit their eggs in large masses (e.g., *S. exigua*, *Choristoneura rosaceana* (Tortricidae) etc.).

In summary, a guild of cursorial hunting spiders were commonly observed feeding on lepidopteran eggs in three field crops in south Texas, although to a greater degree in cotton than in corn or soybeans. The anyphaenid *H. futilis* dominated the guild in most years (3 of 4), but three other species in the families Anyphaenidae (*H. arunda*), Linyphiidae (*G. texana*) and Miturgidae (*C. inclusum*) were frequently observed in one or more years. Absent careful nocturnal observations, most of these spiders pass unrecognized as important biological control agents of lepidopteran pests, much less predators of lepidopteran eggs. Quantification of nocturnal predation and the predators responsible, including the cursorial hunting spiders, is warranted in all agricultural systems to improve our understanding of the natural enemies responsible for the natural control of crop pests.

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