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Seasonal Abundance and Population Structure of Brown Stink Bug (Hemiptera: Pentatomidae) in Farmscapes Containing Corn, Cotton, Peanut, and Soybean

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ABSTRACT  Stink bugs are economically important pests of food and fiber production throughout the southeastern United States. In cotton, stink bugs feed on developing bolls thereby decreasing yield and fiber quality. The brown stink bug, Euschistus servus (Say) (Hemiptera: Pentatomidae), is a common species that is found throughout the southeast and feeds on a variety of wild and agronomic hosts. In this study, the population dynamics and reproductive biology of E. servus were assessed in 1.62–2.83-ha farmscapes planted with corn (Zea mays L.), cotton (Gossypium hirsutum L.), peanut (Arachis hypogaea L.), and soybean [Glycine max (L.) Merr.]. Farmscapes were sampled weekly using whole plant sampling for corn and sweep net sampling in cotton, peanut, and soybean. In 2010, but not 2009, nymphs were classified by instar, and adults were dissected to rate gonads as nonreproductive, intermediate, or reproductive. Regardless of year, stink bugs observed in corn during the spring and early summer and were a mixture of all three reproductive stages. The number of E. servus nymphs and adults was low in all crops during the summer (July, August, and early September). In late September, the number of fifth instars rose sharply followed by an increase in the number of nonreproductive adults, which implies that these adults resulted from reproduction as opposed to immigration. Incidence of late instars and nonreproductive adults was extremely low for corn, cotton, and peanut, and these host plants did not seem to be highly suitable reproductive hosts. Results from this study are useful for pest management programs that focus on reducing stink bug populations on a landscape scale.

KEY WORDS  Euschistus servus, population dynamics, host plant, reproduction, integrated pest management

Stink bugs are polyphagous cosmopolitan pests that damage many agronomic hosts, including cotton (Gossypium hirsutum L.), soybean [Glycine max (L.) Merr.], and corn (Zea mays L.), while also subsisting on wild or nonagronomic hosts that grow throughout the landscape (McPherson and McPherson 2000). Stink bugs are important economic pests of these crops in the southeastern United States and have become primary pests of cotton production (McPherson and McPherson 2000, Greene et al. 2001, Reay-Jones et al. 2010). Understanding the population dynamics of stink bugs in cotton and other agronomic hosts is important because the proximity and type of crop grown adjacent to cotton can affect the value of cotton within a field (Toews and Shurley 2009). Developing cotton bolls are injured by the feeding activity of stink bugs, and this damage decreases the value of cotton by reducing yields and fiber quality (Willrich et al. 2004a,b; Bonmireddy et al. 2007; Toews and Shurley 2009). Although stink bugs have been reported as an occasional pest in cotton fields for more than a century, their recent upsurge is believed to be due the advent of Bacillus thuringiensis technology combined with the boll weevil [Anthonomus grandis grandis Boheman] eradication program that reduced the number of insecticide sprays, which provided indirect control of stink bug populations (Glover 1855, Morrill 1910, Greene and Herzog 1999).

The most serious and abundant species of stink bugs found in Georgia and South Carolina cotton are southern green stink bug, Nezara viridula (L.); Chinavia hilaris (Say); and brown stink bug, Euschistus servus (Say). E. servus is the most widespread among these species and is distributed throughout the eastern, midwestern, and southern portions of the United States from Canada to Florida (Cassidy and Barber 1939, Jones and Sullivan 1982, Munyaneza and McPherson 1994). Previous studies documented many of the life-history characteristics of E. servus, including spring emergence patterns, seasonal abundance on wild or agricultural hosts, and voltinism (Woodside 1946, Rolston and Kendrick 1961, Youther and McPherson 1975, Munyaneza and McPherson 1994, Bundy and McPherson 2000). In addition, studies on the spatial and tem-
poral movement of *E. servus* at the landscape level show that *E. servus* occurs on many host plants throughout the landscape, but it is clustered in its distribution within a field (Steede et al. 2003; Blinka 2008; Reay-Jones et al. 2009, 2010; Smith et al. 2009b; Tillman et al. 2009). Previous studies document the population dynamics of *E. servus* in the context of abundance of nymphs and adults, but little is known about the structure of these populations (e.g., the reproductive capacity of the population). Examining the reproductive status or maturity of the gonads has been used in stink bugs and other insects to assess the age and overall structure of field populations (Brown 1962, Kiritani 1963, Cinereski and Chiang 1968, Toscano and Stern 1980). Toscano and Stern (1980) showed that examining the reproductive condition of *Euschistus conspersus* Uhler was an effective method for predicting seasonal population patterns and reproductive diapause.

Here, we collected data on the overall phenology and reproductive status of stink bugs in adjacent plantings of corn, cotton, peanut (*Arachis hypogaea* L.), and soybean. The purpose of this experiment was to better understand the life cycle and reproductive biology of stink bugs and how individual agronomic crops influence or affect the life-history characteristics of stink bugs. Data were obtained on all stink bug species collected during 2009 and 2010, but this report focuses on the data for *E. servus*; other economically important species will be addressed in subsequent reports.

**Materials and Methods**

**Plot Layout.** Research was conducted in 2009 and 2010 in Georgia on experiment farms operated by the University of Georgia. Replicate plots were located at Midville (32° 52′22.10″ N, 82° 13′23.46″ W), Plains (32° 02′23.53″ N, 84° 22′11.96″ W), and Tifton (3° 31′25.34″ N, 83° 32′52.96″ W). Main plot size varied by location and was between 1.62 and 2.83 ha. The main plot at each location was subdivided into four subplots that were equal in area. Two subplots were rectangular strips that extended the length of the outside edges of the main plot, and the remaining two subplots occupied the area between the two outside subplots (e.g., like that depicted in Fig. 1A). In 2009, cotton was randomly assigned to one of the center subplots and corn was randomly assigned to one of the outside subplots. The remaining subplots were randomly assigned to soybean or peanut. Crops were rotated in 2010 such that cotton was planted on the opposite inside subplot and corn was alternated to the opposite outside subplot. Peanut and soybean were randomly assigned to the remaining two plots. This was done to mimic a typical Southeast Georgia farmscape. Planting, crop management, and harvest dates followed extension-recommended practices for each location. Additional variation in planting date, sampling initiation, and harvest date were governed by local conditions and differences in crop maturity (Table 1). Crops were planted on 0.9-m centers under conventional tillage and all trials were irrigated. No insecticides were applied to the plots after planting.

**Data Collection.** Stink bug sampling occurred within tightly prescribed areas at uniform spacing in a grid pattern. The sampling grid was created by overlaying the main plot with a square grid with grid points 14.2 m apart and then the entire grid was rotated 45° so that the crop rows intersected the diagonals of the sampling grid (Fig. 1A). Grid points were marked in the field by using vinyl flags mounted on a 2.4-m-long fiberglass pole (Agri Drain Corp., Adair, IA). Depending on main plot size, there were 10–12 sample points in each crop. Samples were collected weekly from two rows that were within three rows of the sampling point such that the rows sampled were on opposite sides of the sampling point and four rows apart (Fig. 1B). Dates and weeks of sampling varied by year, location, and crop (Table 1). To avoid sampling the exact same plants in consecutive weeks, sample rows were alternated by week. Corn was sampled by whole plant visual searches including inspection into rolled leaves and inside whorls. Ten corn plants were sampled in each row with five plants before the sampling point and five plants after the sampling point for a total of 20 plants per sample. Stink bugs collected from corn were placed into labeled 15-ml vials or 3.78-liter plastic bags for transport back to the laboratory. Conversely, cotton, soybean, and peanut were sampled using a 38.1-cm sweep net. Technicians executed 20 sweeps per row, with 10 sweeps before the sampling point and 10 sweeps after the sampling point, for a total of 40 sweeps per sample. The entire contents of the sweep

![Fig. 1. (A) Plot layout and arrangement of sampling locations (x’s) at Tifton, GA, in 2010. (B) Illustration of sampling rows, with x denoting the location marked in the field. Rows with the same number were sampled on the same day.](https://academic.oup.com/aesa/article-abstract/104/5/909/16852)
Reproductive organs of males and females were
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structures in their developmental stage. Stink bugs eclose and
reproductive, intermediate, or reproductive based on
visually evaluated in 2010 and given a rating of non-
tergites to expose the abdominal cavity.

**Table 1. Planting, harvest, and sampling dates for 2009 and 2010**

| Yr   | Location | Crop         | Cultivar          | Planting date | Harvest date | First sample date | Last sample date |
|------|----------|--------------|-------------------|---------------|--------------|-------------------|------------------|
| 2009 | Midville | Corn         | DKC67-STRR2       | 23 April      | 7 Sept.      | 16 June           | 4 Aug.           |
| 2009 | Midville | Cotton       | DP 161 B2RF       | 2 June        | 1 Dec.       | 14 July           | 16 Oct.          |
| 2009 | Midville | Peanut       | Georgia Green     | 2 June        | 5 Nov.       | 14 July           | 16 Oct.          |
| 2009 | Midville | Soybean      | Asgrow AG7501     | 2 June        | 29 Nov.      | 14 July           | 16 Oct.          |
| 2009 | Plains   | Soybean      | Asgrow AG7501     | 3 Mar.        | 21 Aug.      | 16 June           | 5 Aug.           |
| 2009 | Plains   | Cotton       | DP 161 B2RF       | 1 June        | 7 Dec.       | 14 July           | 19 Oct.          |
| 2009 | Plains   | Peanut       | Georgia Green     | 1 June        | 4 Oct.       | 14 July           | 19 Oct.          |
| 2009 | Plains   | Soybean      | Asgrow AG7501     | 1 June        | 6 Nov.       | 14 July           | 19 Oct.          |
| 2009 | Tifton   | Corn         | DKC67-STRR2       | 10 April      | 4 Sept.      | 13 July           | 5 Aug.           |
| 2009 | Tifton   | Cotton       | DP 161 B2RF       | 3 June        | 19 Nov.      | 13 July           | 20 Oct.          |
| 2009 | Tifton   | Peanut       | Georgia Green     | 3 June        | 4 Nov.       | 13 July           | 20 Oct.          |
| 2009 | Tifton   | Soybean      | Asgrow AG7501     | 3 June        | 16 Nov.      | 13 July           | 20 Oct.          |
| 2010 | Midville | Corn         | DKC67-ST          | 10 April      | 20 Aug.      | 15 May            | 3 Aug.           |
| 2010 | Midville | Cotton       | DP 1050 B2RF      | 11 May        | 5 Oct.       | 15 June           | 14 Sept.         |
| 2010 | Midville | Peanut       | Tiftguard         | 11 May        | 3 Oct.       | 15 June           | 14 Sept.         |
| 2010 | Midville | Soybean      | Asgrow AG7501     | 11 May        | 8 Nov.       | 15 June           | 21 Oct.          |
| 2010 | Plains   | Corn         | DKC67-ST          | 25 Mar.       | 11 Aug.      | 18 May            | 4 Aug.           |
| 2010 | Plains   | Cotton       | DP 1050 B2RF      | 12 May        | 6 Oct.       | 15 June           | 15 Sept.         |
| 2010 | Plains   | Peanut       | Tiftguard         | 12 May        | 30 Sept.     | 15 June           | 15 Sept.         |
| 2010 | Plains   | Soybean      | Asgrow AG7501     | 12 May        | 28 Oct.      | 15 June           | 21 Oct.          |
| 2010 | Tifton   | Corn         | Asgra Tech 760RR/| 30 Mar.       | 7 Sept.      | 19 May            | 4 Aug.           |
| 2010 | Tifton   | Cotton       | DP 1050 B2RF      | 13 May        | 7 Oct.       | 16 June           | 16 Sept.         |
| 2010 | Tifton   | Peanut       | Tiftguard         | 13 May        | 4 Oct.       | 16 June           | 16 Sept.         |
| 2010 | Tifton   | Soybean      | Asgrow AG7501     | 13 May        | 11 Nov.      | 16 June           | 21 Oct.          |

Vials or plastic bags containing live insects were immediately brought to the laboratory for processing. Samples collected in 2009 were held at −20°C upon arrival; whereas 2010 samples were stored at 4.4°C for up to 48 h for subsequent dissection. Laboratory processing included an assessment of stink bug species, life stage, and quantity, for both years. In 2010, all adults were dissected and the developmental instar of each immature bug was recorded. Adult dissections were performed by pinning each specimen through the pronotum into dissection wax (Carolina Biological, Burlington, NC) that covered the bottom half of a 100-ml glass petri plate. Dissections were performed under a 1% (grams per liter) NaCl salt solution to prevent tissues from rupturing. Sharpened forceps, capable of cutting insect integument, were used to perform dissections by removing the wings and scutellum, cutting the pleural membrane to separate the abdominal tergites and sternites, and removing the tergites to expose the abdominal cavity.

Reproductive organs of males and females were visually evaluated in 2010 and given a rating of non-reproductive, intermediate, or reproductive based on their developmental stage. Stink bugs eclose and emerge as new adults with undeveloped reproductive organs. Reproductive structures in *N. viridula* can become mature in 10 d under optimal conditions, but the time of development for *E. servus* has not been studied (Fortes et al. 2011). Newly emerged nonreproductive males have small testes and a small opaque accessory gland (Fig. 2A). Intermediate males have testes and an enlarged white accessory gland that lacks structural definition (Fig. 2B). Fully mature males have large bright orange testes with an accessory gland that is structurally defined and sacs that are slightly gray or brown (Fig. 2C). Newly emerged nonreproductive females have relatively short and thin ovaries that are bright white in color with no eggs present (Fig. 2D). Intermediate developing ovaries are elongated and contain eggs with a soft chorion that is easily pliable when touched with forceps (Fig. 2E). Fully mature females have greatly expanded ovaries that consume the entire abdominal cavity and are full of eggs with a hardened chorion (Fig. 2F). Females that were postreproductive had elongated ovaries that appear yellowish with follicular relics (image not shown). Images of reproductive organs were captured using a digital camera (EOS Digital Rebel XTi, Canon Inc., Tokyo, Japan) mounted on a dissecting microscope (SMZ 1000, Nikon Co., Tokyo, Japan). Insemination of females was assessed by gently removing the copulatory sac and attached spermatheca. These structures were wet-mounted on a microscope slide using one drop of 1% NaCl (grams per liter) solution and crushed with a coverslip, releasing their contents into the solution. Slides were examined at 200× magnification for the presence of spermatozoa.

**Data Presentation.** Plots of *E. servus* phenology were constructed by pooling the samples by sample date within a crop at each location and then calculating the mean across the three locations. Data are presented by mean because the number of samples within a given crop differed slightly by location. SEs for phenological data were proportional to the mean and are excluded from figures to allow better visibility of all points. Graphs are divided into spring, summer and autumn by using vertical dashed lines that represent the summer solstice and the autumn equinox.
that occurred on the 21 June and 22 September, respectively, for both 2009 and 2010 (U.S. Naval Observatory, Washington, DC). An additional plot documenting the plant phenology in 2010 was constructed using the major physiological events for each crop (Fig. 3).

Statistical Analyses. Statistical analyses were performed to assess the presence of interactions and differences in fixed treatment effects. Data could not be normalized using traditional transformation techniques. Using the principles and examples outlined in Stokes et al. (2000), data (actual counts) were analyzed using a Poisson regression. Data from cotton, soybean, and peanut for 2009 and 2010 were subjected to a repeated measures analysis to examine the differences in the number of adult stink bugs captured among the main effects and interactions of year and crop. Location was random and samples within a crop at a location were considered subsamples. Corn was not included in the analysis because the sampling protocol for corn was different than the protocol used to sample cotton, peanut, and soybean. In addition, populations of E. servus in corn were not compared between 2009 and 2010 because of insufficient data from the spring of 2009. Differences among main effects were further separated using Tukey’s honestly significant difference (HSD) test.

Reproductive stage data from 2010 were analyzed using three separate analyses, based on time of year and temporal sampling opportunity. The first analysis examined data from corn during the spring and early summer; the second analysis examined the data from cotton, peanut, and soybean in the summer for all dates that cotton, peanut, and soybean were sampled and harvested; the third analysis examined the data from soybean in late summer and early fall. Differences among main effects were further separated using Tukey’s honestly significant difference (HSD) test.

Fig. 2. Maturity of E. servus reproductive organs. (A) Nonreproductive male. (B) Intermediate male. (C) Reproductive male. (D) Nonreproductive female. (E) Intermediate female. (F) Reproductive female.

Fig. 3. Crop phenology for corn, cotton, peanut, and soybean in 2010. VT, last branch of tassel visible. Harvest dates for soybean were 26 October–11 November.
concurrently; and the third analysis examined the data from soybean in the autumn for sampling dates that occurred after peanuts and cotton were harvested.

All analyses used a repeated measures Poisson regression model and were performed using PROC GLIMMIX in SAS 9.2 (SAS Institute 2008). Main effects and all interactions were included in the model statement. Year, crop, and reproductive stage were fixed effects, replication was on the level of location, and location was a random effect. When necessary, the slice option in the LSMEANS statement was used to further scrutinize significant interactions; this option allows the investigator to simultaneously test the significance of one factor while holding the second factor fixed. Means and SEs reported in tables were obtained using the ILINK function in the LSMEANS statement, which computes the statistic on the scale of the data as opposed to the fitted Poisson distribution (SAS Institute 2008).

Results

2009 and 2010 Adult Data. Phenology data showed that the pattern in abundance of E. servus adults was similar for 2009 and 2010. Data for adults in 2009 and 2010 show two distinct population peaks that were separated by a period of time where the number of E. servus was low in all crops. The first peak occurred in the late spring and early summer; this peak was initially observed in corn but later observed in soybean after the population of E. servus declined in corn (Fig. 4). Populations of E. servus were low during the summer (July, August, and early September). Adult populations increased during the third week of September for both years and peaked in late September or early October, immediately after the autumn equinox (Fig. 4).

Repeated measures analysis comparing the number of adult stink bugs in cotton, peanut, and soybean for 2009 and 2010 showed differences for the main effects of year (F = 5.71; df = 1, 12; P = 0.03) and crop (F = 92.93; df = 2, 12; P < 0.01), and there was an interaction between crop and year. Further analyses were performed by year to understand the nature of the interaction between year and crop. For 2009 and 2010, there were differences in the number of E. servus among cotton, peanut, and soybean; soybean had the largest mean number of E. servus for both years followed by cotton and then peanut (Table 2). There was not a difference in the abundance of adult stink bugs between cotton and peanut for either 2009 or 2010 (Table 2).

2010 Reproductive Data. Reproductive data from 2010 were recorded for 991 E. servus adults. The percentage of males and females for all E. servus was 49% female and 51% male. Sex ratios for the individual crops were as follows: corn, 44% female and 56% male; cotton, 43% female and 57% male; peanut, 54% female and 46% male; and soybean, 51% female and 49% male. In addition, females were examined to see whether they were inseminated. The percentage of nonreproductive, intermediate, and reproductive females that were inseminated was 4, 90, and 94%, respectively.

Data on the phenology of E. servus broken down by sex and reproductive stage showed that males and females of all three reproductive stages were present in all crops at some time during the year (Figs. 5 and 6). In corn, males attained their peak population abundance before females, and this phenomenon also was observed in cotton during August (Figs. 5A and B and 6A and B). The abundance of males and females peaked at similar times in peanut throughout the year and in soybean during July and August (Figs. 5C and 6C). In soybean during the autumn (September and October), nonreproductive females attained their peak abundance before nonreproductive males (Figs. 5D and 6D).

Analysis of the 2010 reproductive data from spring corn showed differences among reproductive stages.

| Yr | Crop | Mean ± SEM |
|----|------|------------|
| 2009 | Cotton | 0.154 ± 0.036b |
|      | Peanut | 0.092 ± 0.024b |
|      | Soybean | 0.349 ± 0.044a |
| 2010 | Cotton | 0.146 ± 0.015b |
|      | Peanut | 0.094 ± 0.014b |
|      | Soybean | 0.942 ± 0.047a |

Means for crop within a year followed by different letters are different at P < 0.05 Tukey’s HSD test.
(F = 13.39; df = 2, 4; P = 0.02), and there was an interaction between sex and reproductive stage (F = 6.80; df = 2, 4; P = 0.05). No differences were detected among number of nonreproductive, intermediate, or reproductive females, but there was a difference among the reproductive stages for males (F = 16.64; df = 2, 4; P < 0.01). The mean number of reproductive males was greater than the mean number of intermediate males, and the mean number of intermediate males was greater than the mean number of nonreproductive males (Table 3).

Results from the 2010 analysis performed on reproductive data from cotton, peanut, and soybean for all dates that were sampled concurrently showed differences in the effects of crop (F = 76.31; df = 2, 6; P < 0.001) and reproductive stage (F = 31.57; df = 2, 12; P < 0.01), and there was an interaction between reproductive stage and sex (F = 6.48; df = 2, 12; P = 0.01). There were more adults captured in soybean followed by cotton and peanut, respectively (Table 4). Further analyses of the interaction between reproductive stage and sex detected differences for both female and male E. servus among reproductive stages (F = 9.79; df = 2, 12; P < 0.01 and F = 27.58; df = 2, 12; P < 0.01, respectively). In females, there were more reproductive and intermediate females compared with the mean number of nonreproductive females, and there was no difference between the mean number of reproductive and intermediate females (Table 4). In males, there were more reproductive males compared with intermediate and nonreproductive (Table 4).

Analysis of E. servus adults sampled in soybean, after cotton was defoliated and peanut was harvested, showed differences among reproductive stages (F = 64.30; df = 2, 4; P < 0.01). There were more nonreproductive adults (0.750 ± 0.054 [mean ± SEM]) than intermediate (0.066 ± 0.016) or reproductive (0.013 ± 0.008) adults, and there was no difference between the mean number of intermediate and reproductive adults.

**Nymphs.** The population of E. servus nymphs for both years was relatively low in all crops until September with the exception of two clusters of first instars that were collected in corn during the 2010 growing season (Fig. 7). Nymphs attained their peak population abundance in the third week of September for both 2009 and 2010, and the number of nymphs present in soybean was 5 times greater than the greatest number of nymphs observed in any other crop. Data from 2010 on individual instars showed that sweep net samples from soybean contained twice as many fifth instars compared with fourth instars and that there were twice as many fourth instars compared with third instars (Fig. 7E). First and second instars were not recovered in sweep net samples (Fig. 7C-E).
Discussion

Sampling and dissection techniques used in this experiment successfully characterized the annual life cycle of *E. servus*. It is important to note that sweep net sampling has been shown to bias samples by capturing a larger portion of late instars and adults, compared with other sampling techniques (Reay-Jones et al. 2009). Sweep net sampling enhanced the ability to detect late instars and emerging adults in this experiment but was unable to detect when first instars began hatching from eggs (Fig. 7). This study is the first to report the reproductive status of adult *E. servus* coupled with the progressive development of nymphs to clearly delineate generations of *E. servus* from agronomic hosts. Past studies documenting the life history and phenology of *E. servus* in Illinois, Virginia, and Arkansas showed that *E. servus* is bivoltine (Woodside 1946, Rolston and Kendrick 1961, Munyaneza and McPherson 1994). The abundance of *E. servus* also has been associated with plant phenology (Jones and Sullivan 1981, 1982; Reay-Jones 2010). Data presented here agree with the previous studies and indicate that *E. servus* is bivoltine in Georgia and that abundance is influenced by plant phenology.

Data from this study and review of the literature reveals what seems to be a predictable pattern in the seasonal abundance and reproduction of *E. servus*

![Fig. 6. *E. servus* females by reproductive stage for all locations and sampling dates in 2010 for corn (A), cotton (B), peanut (C), and soybean (D). Dashed vertical lines indicate the summer solstice and autumnal equinox.](image_url)

Table 3. Mean comparisons for significant effects for the analysis of adult reproductive data from corn in 2010

| Sex     | Stage       | Mean ± SEM  |
|---------|-------------|-------------|
| Female  | Nonreproductive | 0.092 ± 0.020a |
|         | Intermediate | 0.075 ± 0.019a |
|         | Reproductive  | 0.118 ± 0.023a |
| Male    | Nonreproductive | 0.026 ± 0.011c |
|         | Intermediate | 0.058 ± 0.020b |
|         | Reproductive  | 0.235 ± 0.033a |

Means for reproductive stage within sex followed by different letters are different at *P* < 0.05 Tukey’s HSD test.

Table 4. Mean comparisons for significant effects for the analysis of adult reproductive data from cotton, peanut, and soybean in 2010

| Effect                  | Variable | Mean ± SEM  |
|-------------------------|----------|-------------|
| Crop                    | Cotton   | 0.023 ± 0.003b |
|                        | Peanut   | 0.012 ± 0.003b |
|                        | Soybean  | 0.099 ± 0.006a |
| Sex × stage (female)    | Nonreproductive | 0.014 ± 0.004b |
|                        | Intermediate | 0.040 ± 0.006a |
|                        | Reproductive  | 0.054 ± 0.007a |
| Sex × stage (male)      | Nonreproductive | 0.012 ± 0.005b |
|                        | Intermediate | 0.021 ± 0.004b |
|                        | Reproductive  | 0.084 ± 0.009a |

Means for variables within the same effect with different letters are different at *P* < 0.05 Tukey’s HSD test.
populations that occur in parts of the Midwest and throughout the southeastern United States. The overwintering population of *E. servus* becomes active during late March and early April, before feeding on wild hosts or early agronomic hosts such as wheat (*Triticum aestivum* L.), and these adults then produce the first generation of nymphs from May to July (Jones and Sullivan 1981, 1982; Munyaneza and McPherson 1994; Reay-Jones 2010). Previous studies and this study indicate that the number of adults in agronomic hosts throughout the summer is relatively low, but there is a sharp increase in the number of *E. servus* adults during late September and October; these new adults do not sexually mature, but go on to overwinter (Bundy and McPherson 2000; Gore et al. 2006; Smith et al. 2009a,b).

It is interesting to note that the previous studies and preliminary data from emergence traps in Georgia (M.D.T., unpublished) documented overwintering population emergence within 2 wk of the vernal equinox, and newly emerged adults of the first generation occurred within 4 wk of the summer solstice. In addition, this study and other studies in soybean report the largest populations of *E. servus* within 3 wk of the autumnal equinox (Bundy and McPherson 2000; Gore et al. 2006). Synthesis of these studies suggests that in addition to a sensitivity to crop phenology, *E. servus* has an inherent phenology that is triggered by changing seasons and direction of photoperiod. Thus, the probability of *E. servus* reproducing in a given crop is dependent on the confluence of stink bug and host phenology. This hypothesis would explain why stink bugs are always more abundant in soybean that produce fruit in September, regardless of the maturity group or planting date (Gore et al. 2006).

Using data on the reproductive status of *E. servus* also was useful in determining the role of agronomic hosts in the life cycle of *E. servus*. Data clearly showed that the first generation of *E. servus* adults in corn were not the result of reproduction in corn because there were no nymphs that preceded the first adults found in corn (Fig. 7B). These adults probably migrated to corn from nonagronomic or early season agronomic hosts. Time series data on the reproductive stage over time show that sexually mature males arrived in corn before females. Male stink bugs are known to produce aggregation pheromones that attract females and may facilitate host or mate finding (Aldrich et al. 1991, Borges et al. 1998, Tillman et al. 2010). Females entered corn as nonreproductive and intermediate adults and attained sexual maturity before emigrating out of corn (Figs. 5A and 6A). Corn may be an important adult resource for *E. servus* but seems to be a poor developmental host for *E. servus* nymphs. Although two clusters of first instars were collected in corn, a corresponding peak of late instars and adults was not observed. Tillman (2010) observed that *E. servus* nymphs did not successfully mature into adults in early planted corn, but late planted corn was a suitable host for nymphal development. Data from this experiment suggest that this difference in suitability could be an artifact of the inherent phenology of *E. servus*.
Results from this study strongly suggest that soybean is a highly suitable host for reproduction and that cotton and peanut are poor nymphal hosts for *E. servus* because the number of late instars and newly emerging adults from cotton and peanut was extremely low. Previous studies from Arkansas and Georgia indicate that soybean harbored larger populations of *E. servus* and *N. viridula* in multicrop systems, indicating that soybean may be a more suitable host for nymphal development than peanut, cotton, or corn (Smith et al. 2008, Olson et al. 2011). Data presented here agree with the previous studies and suggest that a majority of *E. servus* observed within cotton and peanut are probably the result of adult movement through the landscape and are not likely to be the result of successful reproduction.

Understanding if the population is a result of reproduction or migration can have implications for pest management strategies and tactics. The large peak of *E. servus* that occurred in soybean during September was probably the result of successful reproduction, as indicated by the large number of fifth instars that preceded the peak of nonreproductive adults (Figs. 5D and 6D and E). Previous reports concluded that the stink bug populations within soybean late in the season were due to migration of stink bug adults (McPherson et al. 2001, Gore et al. 2006). Those studies did not examine the populations for the existence of newly emerged adults and do not report when fifth instars were present in soybean; therefore, it would be unclear whether the majority of individuals within the peak population was due to reproduction, immigration or both. Data presented here are for *E. servus* only and suggest that the majority of adult *E. servus* observed in soybean late in the season emerged from soybean. Populations of other stink bug species in soybean may be due to other factors, but reproductive data for other stink bug species have not yet been reported in the literature. From a pest management perspective, it would be difficult to mitigate a highly mobile adult population from immigrating into a field. However, a large population of relatively nonmobile immatures could be controlled using a well timed insecticide application and this approach could have long-term suppression implications.

*E. servus* and other stink bugs species are cosmopolitan pests that affect a variety of agronomic and nonagronomic hosts, but current management practices recommend insecticide treatment on an individual field basis. Results from this study suggest that *E. servus* populations are not simply building slowly over time, and there are predictable patterns in the reproductive cycle of *E. servus*. Other stink bug species may use agronomic hosts differentially for reproduction or adult resources. Therefore, understanding how and when stink bugs use a particular host may be important for the development of novel management strategies that exploit the biology and behavior of stink bugs, leading to management practices on a landscape or areawide scale.

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