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Distribution of *Zelus longipes* (Hemiptera: Reduviidae) in South Florida Corn Fields and Its Functional Response to Corn-Infesting Picture-Winged Flies (Diptera: Ulidiidae)

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ABSTRACT The milkweed assassin bug, *Zelus longipes* (L.) (Hemiptera: Reduviidae), is a generalist predator and a potential biological control agent of picture-winged flies (Diptera: Ulidiidae), which cause considerable economic damage to sweet corn yields in Florida. We studied the potential of *Z. longipes* as a biocontrol agent of four ulidiid pests in corn fields: *Euxesta stigmatias* Loew, *Euxesta eluta* Loew, *Euxesta annonae* F., and *Chaetopsis massyla* Walker. Within-plant and within-field distributions of *Z. longipes* and ulidiids and functional responses of *Z. longipes* to ulidiid prey were determined. Highest numbers of *Z. longipes* and ulidiids in the R1, R2, and R3 corn stages were generally in the basal or middle leaves at 09:00 h EST, ears at 13:00 h EST, and top and tassel at 17:00 h EST. Hence, there seemed to be a coordinated migration of *Z. longipes* and ulidiids from the lowest to the highest parts of the corn plant during the day. Within the corn field, aggregated (clumped) distributions were most common for *Z. longipes* and ulidiids especially in the later R2 and R3 stages based on Taylor's power law, Iwao's patchiness regression, index of dispersion, and Lloyd's patchiness indices of dispersion. However, predator and prey populations were lower in the R1 stage, and there were inconsistent results for dispersion indices among times of day and between predators and prey. Ulidiid distributions in R1 were mostly regular (uniform) at 13:00 h EST, but aggregated at 09:00 h and 17:00 h. However, *Z. longipes* R1 distributions were mostly aggregated at 13:00 h, but random or regular at 09:00 h and 17:00 h EST. Handling times for male and female *Z. longipes* were 1.0–1.39 h and 0.67–0.97 h, respectively, and each had a type II functional response to *E. stigmatias*, *E. eluta*, and *E. annonae* and consumed about five flies per day. Although the population abundance of *Z. longipes* can vary between seasons, it appears to be a promising biocontrol agent of ulidiid flies in corn.

KEY WORDS within-field distribution, functional response, milkweed assassin bug, *Euxesta*, *Chaetopsis*

Since the 1960s, the United States has been the world's largest producer of sweet corn (*Zea mays* L.) in metric tons (Hansen and Brester 2012). The two sweet corn market production types, fresh-market and processed, were valued at US$836 million and US$336 million, respectively, in 2009 (ERS 2010). From 2004–2009, Florida led the nation in production of fresh-market sweet corn, with 19–27% of the annual crop value (Mossler 2008, ERS 2010). Since the early 1900s, infestation by picture-winged flies (Diptera: Ulidiidae) has plagued sweet corn production in the United States (Barber 1939). Goyal et al. (2010) reported that *Euxesta stigmatias* Loew, *Euxesta eluta* Loew, *Euxesta annonae* F., and *Chaetopsis massyla* Walker (Diptera: Ulidiidae) all attack sweet corn in Florida. The flies oviposit in corn silk, and the larvae have three instars that feed on corn silk, kernels, and the remainder of the cob (Seal et al. 1996, Nuessly and Capinera 2010). Only one maggot and its resulting damage can render a corn cob (and sometimes a truckload of them) unmarketable (D.R.S., personal communication).

Chemical insecticides have been widely used to control adult ulidiid flies, but the other life stages remain protected inside corn ears. The surviving adult flies from adjacent fields can reenter treated corn fields after insecticide application (Goyal 2010); hence, serious injury to corn ears may occur following this reinfestation (Seal 2001). Because of the lack of knowledge on economic thresholds and the failure of insecticides to provide sufficient control of these pests, growers may apply insecticides daily to keep the corn marketable (Goyal 2010). However, awareness about detrimental effects of chemical insecticides is leading to a more widespread use of nonchemical integrated pest management (IPM) options such as biocontrol. Pupal parasitoids of *E. stigmatias* and possibly other corn-infesting ulidiids include *Splangia*

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spp. (Hymenoptera: Pteromalidae) and an unidentified Eurytomid wasp (Hymenoptera: Eurytomidae) (Báez et al. 2010). Kalsi et al. (2014) surveyed corn fields concurrent with the current study and found that nonpredatory arthropods other than ulidiids found in corn ears included *Lobiopa insularis* Castelnau and *Carpophilus lugubris* Murray (Coleoptera: Nitudilidae), an unidentified *Thrips* sp. (Thysanoptera: Thripidae), mites (Acari), muscoid flies (Diptera: Muscidae), roaches (Blattaria), an ant (Hymenoptera: Formicidae), an earwig (Dermaptera: Forficulidae), and a booklouse (Psocoptera). Predators of ulidiids included *Orius insidiosus* Say (Hemiptera: Anthocoridae), *Anotylus insignitus* (Gravenhorst) (Coleoptera: Staphylinidae), *Chrysoperla carnea* Smith (Neuroptera: Chrysopidae), *Zelus longipes* (L.) (Hemiptera: Reduviidae), and potentially other arthropod species (Kalsi et al. 2014). Thus, at least nine nonpredatory and four predatory species other than the ulidiids were found in corn ears concurrent with the current study (Kalsi et al. 2014). *O. insidiosus* is generally the most common of these predators (Kalsi 2011). It feeds on the eggs and larvae and less frequently on the adults of corn-infesting ulidiids, and there are few other known predators of adult flies (Báez et al. 2010, Nuessly and Capinera 2010, Kalsi 2011).

Developing a biocontrol program in an agricultural system requires ecological information on the pest and its natural enemies (Pearce and Zalucki 2006). Monitoring the abundance of predators and prey is often a key option in IPM. To effectively determine densities, it requires choosing the ideal sample size for minimizing costs yet maximizing effectiveness. An effective sample size can also help to determine if economic thresholds have been reached calling for economic investment in pest control. Knowledge of the ecology or physiology of a predator helps when evaluating its potential. Information about the spatial distribution of a pest helps in choosing biocontrol and other IPM techniques, efficient sampling methods, and realistic population models (Boiteau et al. 1979). Goyal (2010) reported on spatial and temporal distributions of corn-infesting ulidiid adults in southern Florida and used Morisita's index to measure the degree of aggregation (Iwao 1968). Other techniques for measuring degrees of aggregation, or indices of dispersion, include Taylor's power law (Taylor 1961), Iwao's patchiness regression (Iwao 1968), the index of dispersion (Clapham 1936, Selby 1965, Perry and Mead 1979), and Lloyd's patchiness regression (Lloyd 1967, Iwao 1968, Xiao et al. 1997). Except for the current study and Kalsi (2011) for *O. insidiosis*, *A. insignitus*, and additional ulidiid eggs and larvae, the Taylor, Iwao, index of dispersion, and Lloyd tests have not been used previously to find spatial distributions of corn-infesting ulidiids or their natural enemies.

The success of a predator depends on factors such as microclimate, ability to forage on surfaces where the prey occurs, prey type and distribution, and interference from other predators (Hassell 1980, Sutherland 1983, Wilson 2010). Predators aggregated around high prey densities exhibit numerical and functional responses. A functional response per unit time is the change in prey consumption in relation to the change in prey density (Hassell 1978, Cogni et al. 2000), and is a behavioral response because it involves searching (Coll and Ridgway 1995). A functional response is the increase in prey consumed as a function of prey offered, and there are three types of responses: types I, II, and III (Holling 1959a). In type I, the rate of prey consumption linearly increases with increasing prey availability at all food densities or at food densities up to a maximum, beyond which the intake rate is constant (Holling 1959a,b). Type II is characterized by a decreased rate of intake with increasing number of prey offered, and it assumes that the consumer (predator) is limited by its ability to process food (Holling 1959a,b). A type III response is similar to a type II because saturation occurs at high prey densities (Holling 1959a,b). However, at low prey densities, the relationship of prey consumed to prey available is accelerating (more than linearly increasing). The accelerating function results from learning time, prey switching, or a combination of both (Holling 1959a,b). The functional response of a predator is important in determining its effectiveness as a biological control agent. Feeding by a predator and possibly prey selection each depend on the investment of energy expressed as two key parameters related to functional response: handling time and attack rate (Krebs and Davies 1993, Juliano 2001). The handling time of a predator for a prey involves the time required to attack, capture, consume, and digest before the predator's hunger motivates another attack (Holling 1963, Thompson 1975). The attack rate of a predator is determined by the probability of occurrence of the predator–prey encounter, the predator attacking on this encounter, and the attack resulting in a successful prey capture (Holling 1963, Thompson 1975).

The milkweed assassin bug, *Z. longipes*, is a generalist predator that feeds by extra-oral digestion (Cogni et al. 2000, Kalsi and Seal 2011), and it consumes arthropods in all the stages of its life (Unigaro 1958). We tested the potential of *Z. longipes* as a biocontrol agent of *E. stigmatias*, *E. eluta*, *E. annonae*, and *C. massyla* adults in corn fields (Fig. 1). To assess the potential of *Z. longipes* to manage ulidiids, we determined their within-plant and temporal distributions to determine how their numbers vary throughout the plant and over time. On a larger field scale, we also determined within-field distributions to find out if they are aggregate, random, or uniform. Different field plot sizes and times were used to help investigate the best monitoring techniques. To complement the field studies, we determined functional responses in the laboratory of male and female *Z. longipes* to *E. stigmatias*, *E. annonae*, and *E. eluta* to examine how increasing prey density relates to prey consumption.

Materials and Methods

The studies were conducted in a field and laboratory at the University of Florida, Tropical Research

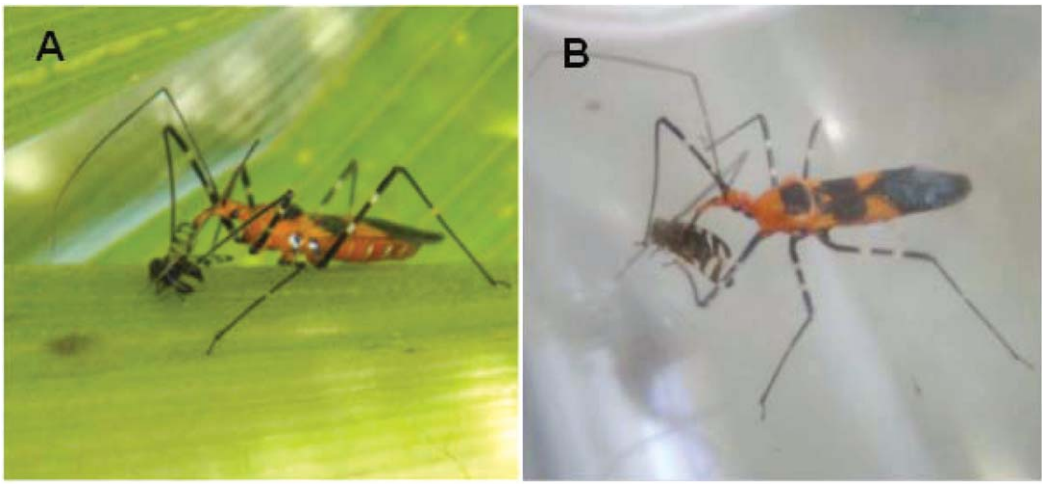

Fig. 1. *Z. longipes* feeding on *Euxesta* spp. flies. (A) Female feeding on *E. stigmatias* in a sweet corn field. (B) Male feeding on *E. annonae* in the laboratory. Photographs by Megha Kalsi.

and Educational Center (TREC), Homestead, FL, from October to December 2010.

Environmental Conditions. At the Florida Automated Weather Network (FAWN) station at Homestead at 60 cm above ground level during the 3-mo period of the tests, mean monthly temperatures (minimum–maximum in parentheses) for October, November, and December 2010, respectively, were 24.1°C (15–32°C), 20.6°C (6–31°C), and 14.2°C (−1–29°C). Relative humidity was 80, 81, and 76% for October, November, and December 2010, respectively. Rainfall was 3.5 cm (1.4"), 7.0 cm (2.8"), and 1.8 cm (0.7") for October, November, and December 2010, respectively (FAWN 2010).

Field Preparation. Studies on the within-plant and within-field distribution patterns of *Z. longipes* were conducted in sweet corn fields. The soil type was Krome gravelly loam soil (loamy-skeletal, carbonatic, hypothermic, lithic, udorthents) that was well drained, had a pH of 7.4–8.4, was 34–76% limestone pebbles (≥2 mm in diameter), and had low organic matter content (<2%; Nobel et al. 1996, Li 2001). Using a garden seeder, seeds of 'Obsession' sweet corn (Seminis Vegetable Seeds, Oxnard, CA) were planted 0.1 m apart within each row and 0.9 m between rows in a 200-m-wide by 20-m-long field on 5 October 2010. Granular fertilizer (N-P-K: 8-16-16, Diamond R fertilizers, Fort Pierce, FL) at the rate of 1,347 kg/ha was applied at planting in a band 0.1 m from the seed rows. Foliar liquid fertilizer (N-P-K: 4-0-8, Diamond R fertilizers) was applied twice at 2.8 kg of N/ha/d to plants at 21 and 35 d after planting (DAP). To control weeds, halosulfuron (Sandea, Gowan Co., Yuma, AZ) was applied 3 wk before planting seeds at 0.20 kg/ha.

The same field was used for within-plant and within-field studies, and there were four replications (blocks) each consisting of thirty 20-m-long rows, hence 600 m of row length per block. Sampling dates and times were the same for within-plant and within-field studies. Both studies were conducted at the following three developmental stages of corn described by Hanway and Ritchie (1984) and Bean (2010): 1) R1 or silking stage (8–9 wk after planting), 2) R2 or blister stage (10–14 d after first silk), and 3) R3 or milk stage (18–22 d after first silk). Sampling began in R1 (56 DAP) because of very low numbers of predators and prey before then and continued during R2 (66 DAP) and R3 (73 DAP) stages. Plants were sampled three times during a single day in each corn stage (09:00–10:00, 13:00–14:00, and 17:00–18:00 h EST). There were hence nine observations in all three corn stages for the within-plant study. The within-field study had 27 total observations (3 corn stages × 3 times × 3 plot sizes). Each sampling involved a separate randomization to determine the plants sampled, and the same set of plants was not intentionally sampled more than once.

Within-Plant Distribution. The experimental field was divided into four equal blocks each consisting of 12 plots, each of which was 4 rows wide × 12.5 m long. In each block, two plots out of 12 were randomly selected, and within each plot, five plants were randomly selected for sampling with randomization by estimation (not by random number tables). Each plant was divided into four strata: basal leaves (lowest three stem nodes), middle leaves (at or above the fourth stem node often surrounding the ears), top leaves and tassel (above the middle leaves), and fruit (corn ears). Numbers of adult and nymph *Z. longipes* and adult ulidiids were recorded separately for each stratum. Sampling involved visually inspecting each plant for ≈1 min, which was ample time because all the plant parts were visible simultaneously. Attention was paid not to disturb the sampled plants to avoid the escape of predators and flies.

Data on within-plant distributions were analyzed separately for each date and time interval. Count data were transformed by $\log_{10}(x+1)$ to improve normality and homogeneity of variance. Data were analyzed using one-way ANOVAs (PROC GLM, SAS Institute

2003). Differences among mean numbers of *Z. longipes* adults and ulidiids on various plant parts were separated by Tukey's HSD tests at $P < 0.05$, but nontransformed means and standard deviations are reported in figures.

Within-Field Temporal and Spatial Distributions. Initially, the field was divided into 48 equal plots (0.0045 ha) as described for the within-plant distribution study. However, for the within-field distribution, initial plots were reorganized to obtain 6, 12, or 24 equal plots by combining 8, 4, and 2 adjacent plots, respectively. To represent sizes potentially useful for field monitoring, there were hence three plot sizes: 90 m^2 (0.009 ha) for the 24-plot field, 180 m^2 (0.018 ha) for the 12-plot field, and 360 m^2 (0.036 ha) for the 6-plot field. The smallest size (90 m^2) resulted from dividing the field into 24 plots by combining 2 adjacent plots from the 48-plot, within-plant study. The intermediate size (180 m^2) resulted from dividing the field into 12 plots and combining 4 adjacent plots, and the largest size (360 m^2) from dividing the field into 6 plots and combining 8 adjacent plots. From each plot, plants were randomly sampled as in the within-plant study with 10 out of 1,000 plants sampled for 90-m^2 plots, 20 out of 2,000 plants for 180-m^2 plots, and 40 out of 4,000 plants for 360-m^2 plots. Each plant was visually checked for ≈0.5–1 min, which was ample time because all plant parts were visible simultaneously. Numbers of *Z. longipes* adults and ulidiids (*E. stigmatias*, *E. eluta*, *E. annonae*, and *C. massyla*) were recorded for each sampled plant.

Distributions in space and time were determined separately for *Z. longipes* and ulidiids. To measure the degree of aggregation for adult *Z. longipes* and ulidiids, four indices of dispersion were calculated for each observation resulting in 36 index values calculated per corn stage within each insect taxon. The indices of dispersion included Taylor's power law (*b;* Taylor 1961), Iwao's patchiness regression (β; Iwao 1968), index of dispersion (*ID;* Clapham 1936, Selby 1965, Perry and Mead 1979), and Lloyd's patchiness index (*LP;* Lloyd 1967, Iwao 1968, Xiao et al. 1997). Indices of dispersion or aggregation for a species are *b*, β, *ID*, and *LP* (Southwood 1978), and each indicates whether the distribution pattern is aggregated, random, or regular (uniform), which occur when $b > 1$, $b = 1$, or $b < 1$, respectively. *ID* values were determined using the sample mean ($\bar{x}$) and variance (s^2; equation 1). Similarly, *LP* was calculated using these variables and the mean number of adult *Z. longipes* or ulidiids per sample (*m;* equation 2). Taylor power law (equation 3) and Iwao patchiness regression parameters (equation 4) were calculated using general linear regression models (Southwood 1978, SAS Institute 2003). Taylor power law determines relationships between $\log \bar{x}$, $\log s^2$, and $\log a$ (sampling factor; equation 3). Iwao patchiness regression relates Lloyd (1967) mean crowding index $[(s^2/\bar{x}) - 1]$, the sample mean ($\bar{x}$), and the index of contagion or tendency toward crowding (α) in equation 4. To determine the within-field distributions for *Z. longipes* and ulidiids using Taylor (*b*) and Iwao (β) indices, we first determined the goodness of fit of data to both linear models using regression coefficients (r^2) from each field test. Then a student's *t*-test helped to determine if the slopes *b* and β were significantly different from 1.0.

$$ID = s^2/\bar{x} \quad [1]$$

$$LP = [(s^2/\bar{x}) - 1]/m \quad [2]$$

$$b = (\log s^2 - \log a)/\log \bar{x} \quad [3]$$

$$\beta = [(s^2/\bar{x}) - 1] + \bar{x} - \alpha \quad [4]$$

Once an index of dispersion was calculated, a "consensus" of the four dispersion indices was determined for each taxon, corn stage, time of day, and plot size. Unlike the index of dispersion (*ID*) and Lloyd (*LP*) tests, Taylor (*b*) and Iwao (β) tests can be checked to determine correlation values (r^2). Because of the greater certainty offered by the r^2 supporting *b* and β, if *b* and β were aggregated and *ID* and *LP* random, the "correct" answer would be aggregated. If *b* and β differed, for example, *b* aggregated and β random, the correct answer would be determined by which index has the higher r^2.

Functional Responses of *Z. longipes* to *E. stigmatias*, *E. eluta*, and *E. annonae*. *Source of Euxesta spp. (Prey).* Colonies began with 100 adults of mixed ages for each species, *E. stigmatias*, *E. eluta*, and *E. annonae*, collected from corn fields in Summer 2010. Each *Euxesta* spp. was reared in a separate cage (31 by 31 by 31 cm), and rearing methods were the same for all the *Euxesta* spp. colonies. Each colony was maintained at 30 ± 5°C, 75 ± 10% relative humidity (RH), and at a photoperiod of 14:10 (L:D) h, and adult flies were supplied with 1% honey solution and fresh water. For oviposition, beet armyworm diet was placed in 28-g plastic cups (BioServe, Beltsville, MD) each attached to the cage ceiling in an inverted position with the diet affixed to the bottom of the cup and the top facing downward to allow oviposition by adults. Fly larvae were provided with an artificial diet designed for beet armyworm (BAW, Southland Co., Lake Village, AR) using methods described by Seal and Jansson (1989). The diet was prepared by adding 0.5 ml honey and 0.2 ml of green food coloring agent (ESCO Food Co., San Jose, CA) to 81 g of dried artificial diet, and all the ingredients were mixed into 465 ml of boiling water. At 24-h intervals, oviposition cups were checked and eggs collected, which were transferred to fresh BAW diet for larval emergence. Newly eclosed first-instar larvae were removed from the egg containers every 24 h and transferred to 28-g plastic cups containing BAW diet and allowed to pupate. Diet cups were checked every 4 h to remove pupae, which were washed gently with tap water to prevent mold development, then air-dried and placed in petri dishes each with a moist paper disk (5 cm in diameter). Petri dishes with pupae were placed in cages (31 by 31 by 31 cm) for adult emergence, with pupae checked every 2 h to collect newly emerged adult flies.

Source of Z. longipes Predators. Male and female *Z. longipes* adults of mixed ages were first collected from

an abandoned sweet corn field infested with ulidiids in Homestead, FL, then placed in an ice chest at 8–10°C to subdue them. *Z. longipes* adults were then brought to the laboratory where four male–female pairs were placed in a 31- by 31- by 31-cm Plexiglas cage held at 30 ± 5°C, 75 ± 10% RH, and at a photoperiod of 14:10 (L:D) h. Twenty ulidiid adults (12–16 h old) were collected from the laboratory colony and added to the cage as a food source for *Z. longipes.* A 10- by 10-cm sponge moistened with tap water was provided in a petri dish (5 cm in diameter) in the cage. As a food source for ulidiids, an inverted glass vial containing 30% sugar solution and plugged with a cotton ball (1 cm in diameter) was also attached to a side wall of the cage. The cage was checked every 24 h for *Z. longipes* eggs, which were transferred to petri dishes (10.5 cm in diameter). Four *Z. longipes* eggs were added to each petri dish along with a moistened filter paper (5 cm in diameter) to prevent desiccation. Petri dishes with eggs were checked every 12 h for first-instar nymphs, which were transferred to other petri dishes (10.5 cm in diameter) each with a moistened filter paper (5 cm in diameter). Each petri dish had two first-instar nymphs of *Z. longipes* that were provided with four ulidiid larvae (second or third instar, 24 h old) daily as a food source. *Z. longipes* nymphs were checked once a day to collect freshly molted second instar and later stages; hence, all the stages were reared in a similar manner until the adult stage. Rearing continued until 16 male–female pairs of *Z. longipes* adults were collected.

Functional Response Experiment. The functional responses of male and female *Z. longipes* adults to *E. stigmatias*, *E. annonae*, and *E. eluta* were measured in plastic cylinders (11.5 cm in width by 14 cm in height) each with cloth mesh (3.5 cm in diameter) in the lid for aeration. Each cylindrical cage was lined with moist foam at the base to avoid desiccation. A glass vial plugged with cotton and containing 5% honey solution was fastened to the cage wall as a food source for the adult flies. Adults of *E. stigmatias*, *E. eluta*, and *E. annonae* were first immobilized by placement at 10°C for 1–2 min. Once immobilized, adult flies were added to the arenas, followed by the addition of *Z. longipes.* Each cylindrical cage had one male or one female adult *Z. longipes*, which was provided with adults of one fly species: *E. stigmatias*, *E. eluta*, or *E. annonae* in groups of 0 (control), 2, 4, 6, 8, or 10 flies. To standardize predator responses, adult *Z. longipes* were starved for 24 h before conducting the test. After a 24-h feeding period, the number of dead flies in each arena was counted, which were considered attacked or fed upon by *Z. longipes* based on observation and comparison with control arenas without predators. There were eight replications at each fly density including the control, but replicates were discarded if the predator died during the 24-h feeding period.

The predation data allowed the calculation of the shapes and types of functional response curves (type I, II, or III), handling times, and attack constants. The type of functional response was found by using polynomial equations describing relationships between initial prey density and the proportion of flies eaten (PROC CATMODE, SAS Institute 2003). The shape of the functional response curve was found using the model in equation 5. Here, N_e is the number of prey eaten, N_0 the initial number of prey, and P_0, P_1, P_2, and P_3 the parameters estimated by PROC CATMODE. If the first estimated parameter (P_1) was negative, the functional response for the predator was a type II, and if the first term was positive, the functional response was type III. Once the type of functional response was determined, data and the resulting mechanistic model were fit to the random predator equation, and the handling time and attack constant parameters were estimated using the NLIN procedure described by Juliano (1993) (PROC NLIN, SAS Institute 2003). In PROC NLIN, a nonlinear, least-square regression of the number of flies eaten versus the number offered was used to estimate and compare different parameters of the functional response. Equation 6 was used for a type II functional response with a the instantaneous search rate or attack constant (time taken by a predator to search for its prey), the handling time (T_h), and the total time available for *Z. longipes* to search for and attack its prey (T). Because the number of adult *E. stigmatias*, *E. eluta*, and *E. annonae* prey declined, as they were consumed without being replaced by new adults, the method of Juliano (1993) was used to fit the data to the random predator equation described by Rogers (1972).

$$N_e/N_0 = \{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)/ [1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)]\} \quad [5]$$

$$N_e = N_0\{1 - \exp[a(T_hN_e - T)]\} \quad [6]$$

Results

Within-Plant Distribution. Although population abundances of *Z. longipes* and ulidiid flies were very low early in the corn vegetative stages, populations increased during the season beginning before the emergence of tassels (male inflorescences; Fig. 2). In the R1, R2, and R3 corn stages, highest numbers of combined nymph and adult *Z. longipes* were generally in the basal or middle leaves at 09:00 h EST, corn ears at 13:00 h EST, and top leaves and tassels at 17:00 h EST. Within-plant distributions of ulidiids were generally similar to *Z. longipes* distributions except at 09:00 h EST, when ulidiids were also most common on ears in addition to the basal and middle leaves. Partly because of this similar within-plant occurrence in the R1, R2, and R3 stages, *Z. longipes* and ulidiids each had significant differences between within-plant locations at each measurement time (09:00, 13:00, and 17:00 h EST; Fig. 2).

During the R1 stage at 09:00 h EST, mean numbers of *Z. longipes* adults on the basal leaves were significantly greater than on the top and tassels (Fig. 2A). Simultaneously, however, mean numbers of ulidiids were significantly greater on the fruit than on the top and tassels (Fig. 2A). During R1 at 13:00 h EST, mean numbers of *Z. longipes* adults and ulidiids were each

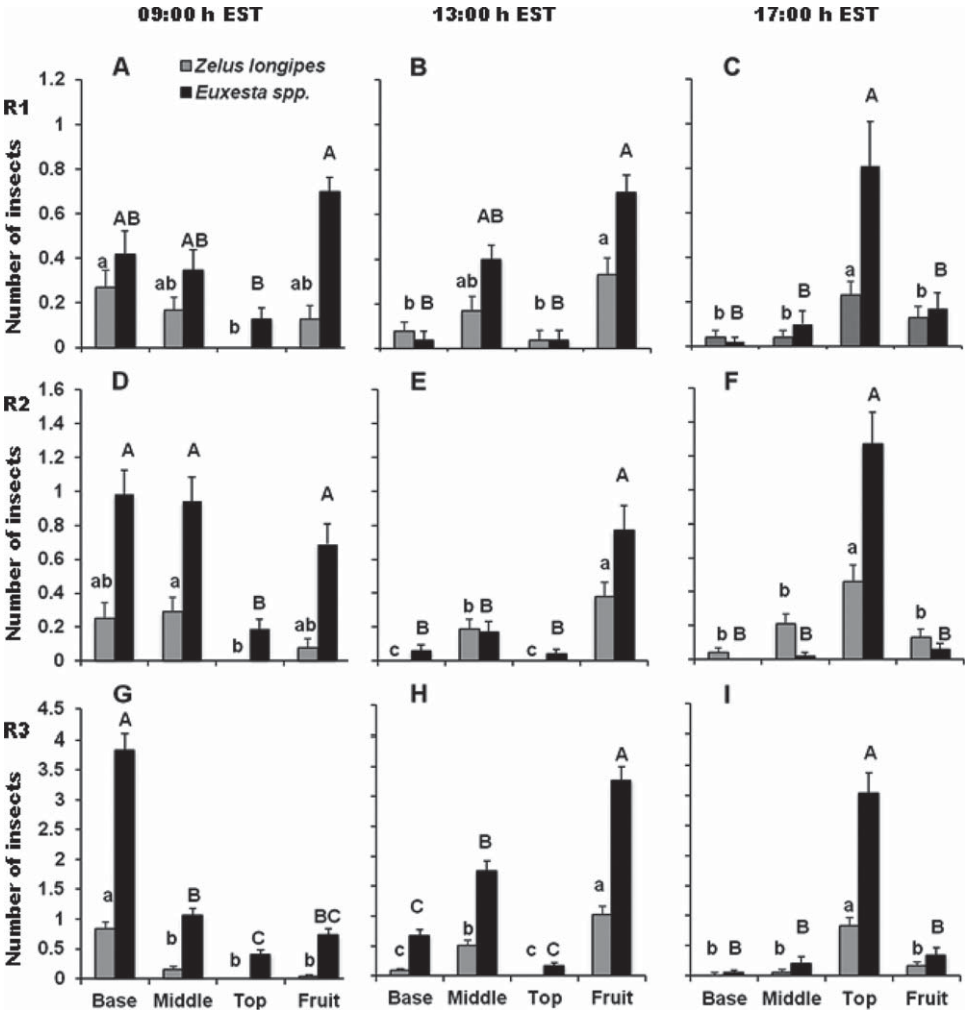

Fig. 2. Mean numbers of combined nymph and adult *Z. longipes* and adult ulidiid flies on different parts of field-grown sweet corn plants per time of day and developmental stage of corn (R1, R2, or R3; Hanway and Ritchie 1984, Bean 2010). Different lower case letters (a, b, and c) indicate significant differences in mean numbers of *Z. longipes* based on one-way ANOVAs followed by Tukey HSD tests. Different upper case letters (A, B, and C) indicate significant differences in mean numbers of *Euxesta* spp. based on one-way ANOVAs followed by Tukey HSD tests ($\alpha = 0.05$). (A) *Z. longipes:* $F = 4.13$; df = 3, 192; $P < 0.072$. *Euxesta* spp: $F = 3.32$; df = 3, 192; $P < 0.021$. (B) *Z. longipes:* $F = 5.19$; df = 3, 192; $P < 0.018$. *Euxesta* spp: $F = 13.17$; df = 3, 192; $P < 0.001$. (C) *Z. longipes:* $F = 4.07$; df = 3, 192; $P < 0.021$. *Euxesta* spp: $F = 15.30$; df = 3, 192; $P < 0.0001$. (D) *Z. longipes:* $F = 4.02$; df = 3, 192; $P < 0.0084$. *Euxesta* spp: $F = 9.23$; df = 3, 192; $P < 0.0001$. (E) *Z. longipes:* $F = 14.09$; df = 3, 192; $P < 0.0001$. *Euxesta* spp: $F = 18.54$; df = 3, 192; $P < 0.0001$. (F) *Z. longipes:* $F = 7.9$; df = 3, 192; $P < 0.0001$. *Euxesta* spp: $F = 41.94$; df = 3, 192; $P < 0.0001$. (G) *Z. longipes:* $F = 32.29$; df = 3, 192; $P < 0.0001$. *Euxesta* spp: $F = 105.9$; df = 3, 192; $P < 0.001$. (H) *Z. longipes:* $F = 27.15$; df = 3, 192; $P < 0.0001$. *Euxesta* spp: $F = 78.96$; df = 3, 192; $P < 0.001$. (I) *Z. longipes:* $F = 18.46$; df = 3, 192; $P < 0.0001$. *Euxesta* spp: $F = 58.53$; df = 3, 192; $P < 0.0001$.

significantly greater on the fruit than on the basal leaves or top and tassels (Fig. 2B). During R1 at 17:00 h EST, mean numbers of *Z. longipes* adults and ulidiids were each greater on the top and tassels, where there were significantly more of each taxon than on the fruit, basal leaves, or middle leaves (Fig. 2C).

During the R2 stage at 09:00 h EST, mean numbers of *Z. longipes* adults were significantly greater on the middle leaves than on the top and tassels (Fig. 2D). Simultaneously, mean numbers of ulidiids were significantly greater on the basal leaves, middle leaves, and fruit than on the top and tassels (Fig. 2D). During R2 at 13:00 h EST, mean numbers of *Z. longipes* adults and ulidiids were each significantly greater on the fruit than on the middle leaves, basal leaves, or top and tassels (Fig. 2E). During the R2 stage at 17:00 h EST, mean numbers of ulidiids and *Z. longipes* adults were each significantly greater on the top and tassels than on the basal leaves, middle leaves, or fruit (Fig. 2F).

During the R3 stage at 09:00 h EST, mean numbers of *Z. longipes* adults and ulidiids were each significantly greater on the basal leaves than on the middle

Table 1. Ulidiid indices of dispersion—Taylor's power law, Iwao's patchiness regression, index of dispersion, and Lloyd's patchiness index for ulidiids recorded in a corn field at three crop growth stages, three times of the day, and three plot sizes

Corn stage[a]	Time (hours) EST	Plot size (m^2)	Overall disp.[b,c]	Taylor's power law[c]		Iwao's patchiness regression[c]		Index of dispersion[c]	Lloyd's patchiness index[c]
				b	r^2	β	r^2	*ID*	*LP*
R1	09:00	360	AGG	3.51 agg[c]	0.98	3.09 agg	0.97	1.87 agg	1.87 agg
R1	09:00	180	AGG	1.31 agg	0.91	1.54 agg	0.92	1.91 agg	1.92 agg
R1	09:00	90	AGG	1.14 agg	0.82	1.22 agg	0.75	1.98 agg	1.98 agg
R1	13:00	360	REG	0.67 reg	0.98	0.69 reg	0.96	0.63 reg	0.67 reg
R1	13:00	180	REG	0.33 reg	0.92	0.48 reg	0.91	0.76 reg	0.78 reg
R1	13:00	90	REG	0.28 reg	0.67	0.36 reg	0.66	0.85 reg	0.95 ran
R1	17:00	360	AGG	2.89 agg	0.97	2.98 agg	0.98	1.50 agg	1.51 agg
R1	17:00	180	AGG	1.90 agg	0.79	1.83 agg	0.85	1.47 agg	1.47 agg
R1	17:00	90	AGG	1.15 agg	0.71	1.85 agg	0.73	1.51 agg	1.49 agg
R2	09:00	360	AGG	1.63 agg	0.90	1.45 agg	0.91	1.06 ran	1.05 ran
R2	09:00	180	AGG	1.73 agg	0.71	1.76 agg	0.80	1.05 ran	1.06 ran
R2	09:00	90	AGG	1.56 agg	0.75	1.59 agg	0.75	1.01 ran	1.06 ran
R2	13:00	360	AGG	2.4 agg	0.98	3.23 agg	0.97	1.76 agg	1.65 agg
R2	13:00	180	AGG	1.50 agg	0.97	1.73 agg	0.98	1.63 agg	1.55 agg
R2	13:00	90	AGG	1.39 agg	0.68	1.18 agg	0.58	1.72 agg	1.63 agg
R2	17:00	360	AGG	5.54 agg	0.99	5.90 agg	0.99	1.4 agg	1.31 agg
R2	17:00	180	AGG	3.48 agg	0.65	3.22 agg	0.61	1.45 agg	1.34 agg
R2	17:00	90	AGG	1.40 agg	0.61	1.48 agg	0.60	1.48 agg	1.37 agg
R3	09:00	360	AGG	4.18 agg	0.96	1.4 agg	0.93	1.77 agg	1.96 agg
R3	09:00	180	AGG	3.47 agg	0.91	1.15 agg	0.90	1.70 agg	1.95 agg
R3	09:00	90	AGG	2.42 agg	0.97	1.08 agg	0.95	1.42 agg	1.89 agg
R3	13:00	360	AGG	5.93 agg	0.93	5.96 agg	0.92	1.0 ran	1.04 ran
R3	13:00	180	AGG	4.57 agg	0.85	4.12 agg	0.68	1.06 ran	1.02 ran
R3	13:00	90	AGG	2.80 agg	0.79	2.47 agg	0.57	1.14 agg	1.06 ran
R3	17:00	360	AGG	2.79 agg	0.96	2.78 agg	0.95	2.12 agg	1.32 agg
R3	17:00	180	RAN	1.06 ran	0.67	1.05 ran	0.83	1.94 agg	1.28 agg
R3	17:00	90	REG	0.46 reg	0.58	0.73 reg	0.54	2.12 agg	1.39 agg

[a] From Hanway and Ritchie (1984) and Bean (2010).
[b] Overall dispersion estimate based on "consensus" of the four indices.
[c] Dispersion variables (b, β, *ID*, *LP*, and overall dispersion). Aggregated distribution (AGG or agg): b, etc., significantly >1 ($P \leq 0.05$); random (RAN or ran): b, etc., not significantly different from 1 ($P > 0.05$); and regular or uniform (REG or reg): b, etc., significantly <1 ($P \leq 0.05$).

leaves, fruit, or top and tassels (Fig. 2G). At 13:00 h EST, mean numbers of *Z. longipes* and ulidiids were each significantly greater on the fruits than on the middle leaves, basal leaves, or top and tassels (Fig. 2H). At 17:00 h EST in R3, mean numbers of *Z. longipes* and ulidiids were each significantly greater on the top and tassels than on the fruit, middle leaves, or basal leaves (Fig. 2I).

Within-Field Temporal and Spatial Distributions. *Ulidiids.* Indices for Taylor's power law (b), Iwao's patchiness regression (β), index of dispersion (*ID*), and Lloyd's patchiness index (*LP*) were each significantly >1.0 for all three plot sizes in R1 at 09:00 and 17:00 h EST, indicating aggregated distributions (Table 1). However, at 13:00 h EST, all four dispersion indices were generally significantly <1.0 showing mostly regular distributions, except for *LP* of 90-m^2 plots, which was not significantly different from 1.0, indicating a random distribution. Hence, in the R1 corn stage for ulidiids, "consensus" distributions for all three plot sizes were aggregated at 09:00 and 17:00 h EST and regular at 13:00 h EST (Table 1).

For R2 ulidiid distributions at 09:00 h EST in all three plot sizes, *ID* and *LP* were not significantly different from 1.0, indicating random distributions, but b and β were each significantly >1.0, indicating aggregated distributions. However, R2 distributions at 13:00 h and 17:00 h EST were all aggregated. Thus, in R2, ulidiid "consensus" distributions for all times and plot sizes were aggregated (Table 1).

During R3 at 09:00 h EST, all four indices for all three plot sizes yielded aggregated distributions for ulidiids (Table 1). In R3 at 13:00 h for 180-m^2 and 360-m^2 plots, however, b and β showed aggregated distributions, while *ID* and *LP* were random; the 90-m^2 plots found b, β, and *ID* distributions were aggregated with *LP* random. Thus, in R3 at 13:00 h, distributions were aggregated for all plot sizes. In R3 at 17:00 h EST for 360-m^2 plots, all four indices had aggregated distributions; for 180-m^2 plots, b and β showed random distributions, while *ID* and *LP* were aggregated; and for 90-m^2 plots, b and β had regular distributions, but *ID* and *LP* were aggregated. Hence, "consensus" distributions for R3 ulidiids were aggregated for all times and plot sizes except for 180-m^2 and 90-m^2 plots at 17:00 h, which were random and regular, respectively (Table 1).

Zelus Longipes. During R1 at 09:00 h for the 90-m^2 and 360-m^2 plots, b and β were each significantly <1.0, indicating regular distributions, while *ID* and *LP* values were not significantly different than 1.0 with random distributions, but for 180-m^2 plots, all four indices showed regular distributions (Table 2). In R1 at 13:00 h for the 180-m^2 and 360-m^2 plots, all four indices showed aggregated distributions, but for 90-m^2 plots, b was regular, β aggregated, and *ID* and *LP* distribu-

Table 2. *Z. longipes* adult indices of dispersion—Taylor's power law, Iwao's patchiness regression, index of dispersion, and Lloyd's patchiness index recorded in a corn field at three crop growth stages, three times of the day, and three plot sizes

Corn stage[a]	Time (hours) EST	Plot sizes (m^2)	Overall disp.[b,c]	Taylor's power law[c]		Iwao's patchiness regression[c]		Index of dispersion[c]	Lloyd's patchiness index[c]
				b	r^2	β	r^2	*ID*	*LP*
R1	09:00	360	REG	0.48 reg	1.0	0.83 reg	0.99	0.96 ran	0.93 ran
R1	09:00	180	REG	0.65 reg	0.71	0.60 reg	0.78	0.84 reg	0.81 reg
R1	09:00	90	REG	0.71 reg	0.74	0.73 reg	0.76	0.95 ran	0.99 ran
R1	13:00	360	AGG	2.65 agg	0.75	5.78 agg	0.91	1.17 agg	1.45 agg
R1	13:00	180	AGG	1.07 agg	0.85	1.75 agg	0.83	1.17 agg	1.34 agg
R1	13:00	90	RAN?[d]	0.88 reg	0.76	1.58 agg	0.72	1.06 ran	1.03 ran
R1	17:00	360	REG	0.89 reg	0.83	0.86 reg	0.89	0.82 reg	0.56 reg
R1	17:00	180	REG	0.85 reg	0.76	0.79 reg	0.76	0.86 reg	0.65 reg
R1	17:00	90	REG	0.72 reg	0.75	0.60 reg	0.7	0.90 ran	0.76 reg
R2	09:00	360	AGG	1.38 agg	0.98	2.4 agg	0.99	2.15 agg	2.96 agg
R2	09:00	180	AGG	1.47 agg	0.99	2.06 agg	0.94	1.67 agg	1.82 agg
R2	09:00	90	AGG	1.37 agg	0.85	1.37 agg	0.74	1.74 agg	2.27 agg
R2	13:00	360	AGG	1.66 agg	0.97	2.30 agg	0.96	1.15 agg	1.24 agg
R2	13:00	180	AGG	1.31 agg	0.98	1.62 agg	0.98	1.18 agg	1.27 agg
R2	13:00	90	AGG	1.08 agg	0.87	1.02 ran	0.68	1.14 agg	1.24 agg
R2	17:00	360	AGG	2.06 agg	0.96	2.83 agg	0.98	1.44 agg	1.47 agg
R2	17:00	180	RAN?[d]	1.04 ran	0.83	1.10 agg	0.74	1.12 agg	1.35 agg
R2	17:00	90	AGG	1.10 agg	0.75	1.13 agg	0.79	1.04 ran	1.07 agg
R3	09:00	360	AGG	1.27 agg	0.99	1.20 agg	0.99	1.15 agg	1.09 agg
R3	09:00	180	AGG	2.79 agg	0.99	3.27 agg	0.99	1.04 ran	1.12 agg
R3	09:00	90	AGG	1.97 agg	0.79	2.06 agg	0.59	1.20 agg	1.19 agg
R3	13:00	360	AGG	2.58 agg	0.99	3.02 agg	0.98	1.32 agg	1.28 agg
R3	13:00	180	AGG	1.5 agg	0.97	1.62 agg	0.99	1.34 agg	1.27 agg
R3	13:00	90	RAN	0.44 reg	0.12	1.02 ran	0.57	1.31 agg	1.16 agg
R3	17:00	360	AGG	1.43 agg	0.98	1.58 agg	0.99	1.59 agg	1.49 agg
R3	17:00	180	AGG	1.87 agg	0.99	2.1 agg	0.98	1.53 agg	1.37 agg
R3	17:00	90	AGG	1.59 agg	0.83	2.01 agg	0.63	1.63 agg	1.41 agg

[a] From Hanway and Ritchie (1984) and Bean (2010).
[b] Overall dispersion estimate based on "consensus" of the four indices.
[c] Dispersion variables (*b*, β, *ID*, *LP*, and overall dispersion). Aggregated distribution (AGG or agg): *b*, etc., significantly >1 ($P \leq 0.05$); random (RAN or ran): *b*, etc., not significantly different from 1 ($P > 0.05$); and regular or uniform (REG or reg): *b*, etc., significantly <1 ($P \leq 0.05$).
[d] The "consensus" value was difficult to estimate and is somewhat uncertain.

tions were random. In R1 at 17:00 h for the 180-m^2 and 360-m^2 plots, all four indices showed regular distributions, but for 90-m^2 plots, *b*, β, and *LP* were regular, while *ID* was random. Overall, "consensus" distributions for *Z. longipes* in R1 for all plot sizes at 09:00 h and 17:00 h were regular and at 13:00 h were random for 90-m^2 plots and aggregated for 180-m^2 and 360-m^2 plots (Table 2).

In R2 at 09:00 for all plot sizes, all dispersion indices indicated aggregated distributions (Table 2). In R2 at 13:00 for 180-m^2 and 360-m^2 plots, all dispersion indices also showed aggregated distributions. In R2 at 13:00 h for the 90-m^2 plots, however, *b*, *ID*, and *LP* were aggregated, while β was random. Taylor's r^2 = 0.87 for *b* (aggregated) was larger than Iwao's $r^2 = 0.68$ for β (random); hence, the "consensus" distribution for R2 at 13:00 h for 90-m^2 plots was aggregated. In R2 at 17:00 h for 360-m^2 plots, all dispersion indices yielded aggregated distributions, but for 180-m^2 plots, *b* had a random distribution with β, *ID*, and *LP* aggregated. Taylor's $r^2 = 0.83$ for *b* (random) was larger than Iwao's $r^2 = 0.74$ for β (aggregated), indicating a random "consensus" distribution for R2 at 17:00 h for 180-m^2 plots. During R2 at 17:00 h for 90-m^2 plots, *b*, β, and *LP* each had aggregated distributions, while *ID* was random. Hence, except for a random distribution with 180-m^2 plots at 17:00 h, *Z. longipes* showed aggregated "consensus" distributions at all times and plot sizes in R2 (Table 2).

During R3 at 09:00 h for the 90-m^2 and 360-m^2 plots, all dispersion indices showed aggregated distributions, but for 180-m^2 plots, *b*, β, and *LP* were aggregated while *ID* was random (Table 2). In R3 at 13:00 h for the 180-m^2 and 360-m^2 plots, all dispersion indices yielded aggregated distributions; however, for 90-m^2 plots, *b* had a regular distribution, but the poor fit ($r^2 = 0.12$) suggested that it may have been random or aggregated instead. However, β was random with a more confident $r^2 = 0.57$, and *ID* and *LP* each had aggregated distributions. In R3 at 17:00 h EST, all four indices for all three plot sizes indicated aggregated distributions. For *Z. longipes* in R3, overall "consensus" distributions at all times and plot sizes were aggregated except for R3 at 13:00 h for 90-m^2 plots, which was random.

Functional Responses of *Z. longipes* to *E. stigmatias*, *E. eluta*, and *E. annonae*. *Z. longipes* males had mean handling times (T_h) for *Euxesta* spp. of 1.0–1.4 h, while females handled *Euxesta* spp. in 0.67–0.97 h (Table 3). Mean attack constants (*a*) for male and female *Z. longipes* were 0.05–0.07. *Z. longipes* male and female adults each showed a type II functional response to adults of *E. stigmatias*, *E. eluta*, and *E. annonae* (Table 3; Fig. 3). Each type II response curve exhibited a "plateau" or "leveled off" after adding 6–10 flies, thus

Table 3. Functional responses and parameters of *Z. longipes* to adults of corn-infesting *Euxesta* spp.

Sex of *Z. longipes*	Functional type	Prey: *Euxesta* spp.	Handling time T_h (h)[a]	Attack constant a (h^{-1})[a]
Male	II	*E. stigmatias*	1.12 ± 2.25	0.07 ± 0.03
Male	II	*E. eluta*	1.0 ± 1.23	0.06 ± 0.02
Male	II	*E. annonae*	1.39 ± 1.27	0.07 ± 0.02
Female	II	*E. stigmatias*	0.97 ± 1.25	0.06 ± 0.02
Female	II	*E. eluta*	0.67 ± 1.81	0.05 ± 0.03
Female	II	*E. annonae*	0.82 ± 1.36	0.05 ± 0.02

[a] Mean ± SE.

indicating maximum numbers of prey were consumed following addition of at least six flies. Hence under laboratory conditions, males had maximum prey consumptions of 4.8–5.3 flies per day, while females consumed up to 5.1–5.6 flies per day (Table 3).

Discussion

Sweet corn provides a breeding substrate for ulidiid flies; females prefer to lay eggs inside newly emerged silk (corn stigmas and styles) near the tips of corn ears, and oviposition decreases as the corn silk ages (Seal et al. 1996). In the current study, the abundance of ulidiids was very low before silking, which may have resulted from a lack of suitable oviposition sites. As plant growth proceeded from R1 to R3 stages, abundances of *Z. longipes* and ulidiids increased considerably, which concurs with results of Seal et al. (1996) who found the density of *E. stigmatias* continued to increase until 3 wk after anthesis. Increasing predator density with increasing numbers of prey was also supported by Rogers (1972). In the current study, higher abundances of *Z. longipes* and ulidiids with advancing corn stage may have resulted from earlier reproduction, continued abundance of food, and movement of predator and prey within the field.

Early in the day at 09:00 h, both predator and prey seemed to be most abundant on the lower plant parts, the base and middle. As the day progressed, both were most common on the fruit, and they continued their apparent "migration" to the highest plant parts, the top and tassel, toward the end the day at 17:00 h. These results were supported by Seal et al. (1996), who found that *E. stigmatias* showed peak oviposition from 09:00–13:00 h EST when gravid females aggregated around the lower and middle parts of corn plants to oviposit in silk channels. Seal et al. (1996) also observed variation in the diel pattern of mating behavior, with most *E. stigmatias* mating in the evening near the tassel. Although we did not measure the correlation statistically, the similar within-plant distributions of ulidiids and *Z. longipes* would seem to provide the predators better access to the prey than if they were found on different plant parts. This may facilitate increased prey consumption compared with if no such coincidence existed, although this was not measured quantitatively.

Ulidiids and adults of *Z. longipes* were first observed 2 wk after corn planting, when predator and prey populations were low but beginning to increase on corn plants. The indices from Taylor's power law, Iwao's patchiness regression, index of dispersion, and

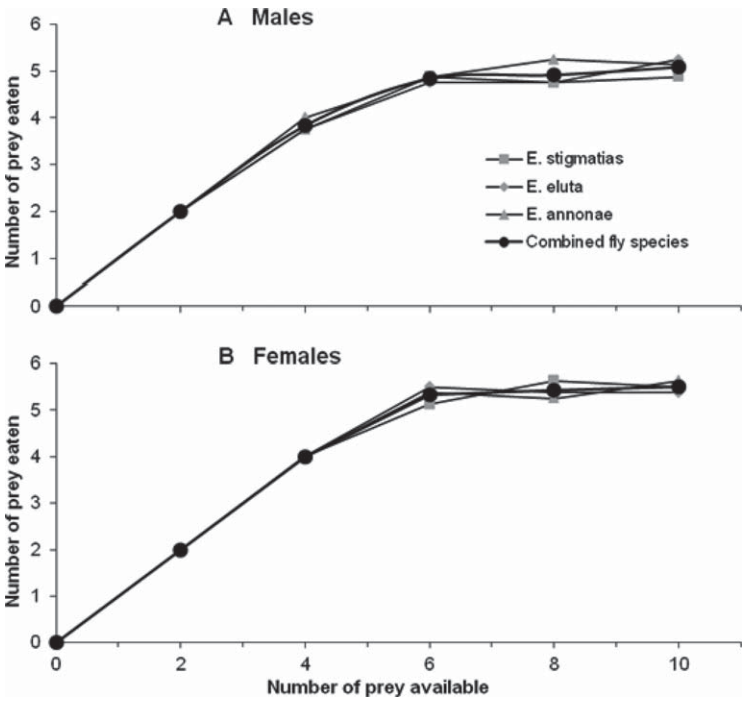

Fig. 3. Type II functional responses of (A) male and (B) female *Z. longipes* to *E. stigmatias*, *E. eluta*, *E. annonae*, and the combination of these fly species.

Lloyd's patchiness appeared to show varying distribution patterns during R1 and more consistently aggregated distributions during R2 and R3. The r^2 values generally indicated that the larger the plot size and the number of plants sampled, the more confidence was found in results of b and β, the only variables that could be checked with r^2 to determine confidence levels. For example, for ulidiids at17:00 h in R3, r^2 distributions (b, β) were (0.96, 0.95), (0.67, 0.83), and (0.58, 0.54) for the 360-, 180-, and 90-m^2 plot sizes, respectively. Therefore, to randomly sample ulidiids and *Z. longipes* on 1% of the plants in a field, we recommend using plots of at least 180 m^2 to obtain reliable indices of dispersion and possibly for monitoring. In the R1 stage, ulidiid indices were aggregated at 09:00 or 17:00 h and regular at 13:00 h EST, but for *Z. longipes*, they were regular at 09:00 and 17:00 h and aggregated for 360 m^2 and 180 m^2 plots at 13:00 h or random for 90-m^2 plots. Aggregation patterns appeared inconsistent between times of day and between *Z. longipes* and ulidiids with R1 indices for *Z. longipes* mostly the reverse of ulidiid indices. *Z. longipes* may have depleted its prey in the areas sampled causing low prey density, or it may not yet have arrived where the prey density was high, making it appear like the predators were not where the prey was. We randomly sampled 1% of the plants per plot; thus, larger sample sizes may have reduced this problem increasing confidence levels (r^2) or causing more similar indices of dispersion between times of day for *Z. longipes* and ulidiids or both. Rogers (1972) noted that to find prey, predators adopt random search strategies that are independent of prey distribution. Predators also have random attack strategies, which are functions of host density. In R2 and R3, *Z. longipes* and ulidiids were well established in the field, and the high prey populations densities tended to be aggregated. Hassell (1978) agreed with this observation by reporting that at high densities, many predators show aggregated distributions.

On soybeans *Glycine max* (L.) Merrill and alfalfa *Medicago sativa* L. (Fabaceae), Pearce and Zalucki (2006) noted plant damage, counted herbivores and predators such as wolf spiders (Lycosidae), and used eggs of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) to find predation rates. They found that ground-dwelling and foliage-dwelling predators were often aggregated into patches ≈40 m across within apparently uniform soybean fields. However, predator aggregation did not correlate consistently with pest aggregation, plant damage, or predation rate. The most consistently associated spatial pattern of predator abundance and a parameter measured was between foliage-dwelling predators and pests, with significant results in four of the seven test grids. Generalist predators were rarely distributed randomly, and field edges and adjacent crops influenced the within-field predator abundances (Pearce and Zalucki 2006). Hence, the predominantly aggregated distributions of predators and prey found in middle and later corn stages of the current study seem to have also been observed by Pearce and Zalucki (2006), especially with predators.

As suggested by their different formulas, the four indices of dispersion measure differently. Each index was developed using organisms other than *Z. longipes* or ulidiids, and the current study was the first application of the indices to ulidiids or *Z. longipes.* The Taylor's power law (b) was developed and used on plants and aphids (Taylor 1961, Southwood 1978), Iwao's patchiness regression (β) with insect colonies (Iwao 1968, Southwood 1978), index of dispersion (*ID*) mainly by plant ecologists (Perry and Mead 1979), and Lloyd's patchiness index *(LP)* with animals in continuous quadrants (Lloyd 1967, Southwood 1978). When differences occur between index values, results of *ID* and *LP* usually have less merit than b and β because the latter two can be checked with correlation tests (r^2). When comparing b and β, the index with the higher r^2 is statistically more likely to represent the correct dispersion. For *Z. longipes* in R1 at 13:00 h for 90-m^2 plots, Taylor's $r^2 = 0.76$ was greater than Iwao's $r^2 = 0.72$; thus, Taylor's $b = 0.88$ (regular) was more likely correct than Iwao's $\beta = 1.58$ (aggregated). However, the r^2 values (0.76 and 0.72) were very similar, and *ID* and *LP* had random distributions (between aggregate and regular). Hence, the most likely distribution for *Z. longipes* at 13:00 h in R1 for 90-m^2 plots seems to have been random. *Z. longipes* indices in R2 at 17:00 h for 180-m^2 plots were also difficult to evaluate because $b = 1.04$ (random) had the highest r^2 value (0.83), while all the other values including β ($r^2 = 0.74$) were aggregate. For *Z. longipes*, R1 indices at 13:00 h for 90-m^2 plots and R2 indices at 17:00 h for 180-m^2 plots seem to have been random, but each was somewhat unclear.

While indices of dispersion from field studies indicate degrees of aggregation of predators or prey individually, a laboratory study with a functional response applies the interaction of increasing prey density with a given number of predators in a controlled laboratory environment. According to Cohen and Tang (1997), decreased predator-to-prey weight ratios typically cause increased handling times, which is also suggested by our findings. Males of *Z. longipes* required longer handling times than females possibly because they are smaller than females (Hart 1986, Kalsi and Seal 2011).

Although *Z. longipes* is a generalist predator (Cogni et al. 2000, Kalsi and Seal 2011), it exhibited a type II functional response toward all three *Euxesta* spp. However, generalist predators typically exhibit a type III functional response (Murdoch and Oaten 1975, Hassell et al. 1977) because they are independent of prey density and can switch from one prey type to another (Hassell et al. 1977). A predator with a type II response would appear to be more effective than a type III toward ulidiids because the latter would be more likely to switch to nontarget pests, thus decreasing its effectiveness toward ulidiids. However, a type III would be more likely to survive when the target pest is absent because it could switch to nontarget pests for survival. Hence, an ideal biocontrol agent may have a type III response but with ulidiids as the preferred prey. We found that *Z. longipes* had a type

II response because the experiment involved a no-choice test with only one prey type regardless of which *Euxesta* sp. was supplied; hence, the predator could not switch to other prey types. Because *Z. longipes* were reared on ulidiid larvae but provided with adult flies in the functional response experiment, learning presumably occurred rapidly because the number of prey offered and the number eaten were almost identical in the 24-h test period. There was no evidence of a sigmoid shape until the curve flattened presumably because of satiation. Hence, having previously experience with adult flies instead of larvae or a longer test period seems unlikely to have resulted in a different shape to the functional response curve. Because of the no-choice environment, the predator learning to switch prey species would have been more difficult (or impossible) to demonstrate compared with an environment with multiple prey species because only one prey type was offered. Because other potential prey species coexisted with ulidiids in corn ears (Kalsi et al. 2014), if the experiments were performed in a more field-like setting, *Z. longipes* may have exhibited a type III functional response given its ability to choose alternative prey; hence, different results may have occurred.

In a corn field survey concurrent with the current study, Kalsi et al. (2014) found *Z. longipes* in the fall, but not in the spring or summer 2010, while other predatory species such as *O. insidiosus* and *A. insignitus* occurred in two or in all three seasons. A major disadvantage of *Z. longipes* may hence be its sporadic occurrence, although in addition to corn, C.G.M. (personal observation) has often seen it on south Florida shrubs such as *Murraya paniculata* (L.) Jack (Rutaceae), and it may be widespread. In an environment where few other predators consume adult ulidiid flies, we found that *Z. longipes* tended to have clumped (aggregated) distributions that coincided with aggregated distributions shown by the ulidiid prey. Furthermore, *Z. longipes* and ulidiids showed good spatial coincidence and were found on similar parts of the corn plant at similar times of day. *Z. longipes* rapidly learned to take adult ulidiids and had a maximum consumption of 4.8–5.6 flies in a 24-h period at 30 ± 5°C and 75 ± 10% RH. Yet it is a generalist predator and can presumably survive on other insect species when ulidiids are scarce. Hence, we believe *Z. longipes* is a promising biocontrol agent of ulidiid flies in corn. Additional studies might investigate effects of *Z. longipes* on corn yields, its use in augmentative or mass-release programs, its ability to regulate ulidiids below economic thresholds, its effectiveness as a fly predator and in suppressing fly populations in the field, if it selects flies over other prey, and whether its abundance or the ease of capturing and killing prey causes it to be effective. These findings may allow comparisons with other ulidiid predators such as *O. insidiosus* and can help in understanding the effectiveness of *Z. longipes* in controlling the flies.

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