J Pest Sci (2017) 90:433–445
DOI 10.1007/s10340-016-0802-3

ORIGINAL PAPER

Attack and defense movements involved in the interaction of *Spodoptera frugiperda* and *Helicoverpa zea* (Lepidoptera: Noctuidae)

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Received: 13 May 2016 / Revised: 13 July 2016 / Accepted: 26 July 2016 / Published online: 9 August 2016

Abstract The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) and the corn earworm, *Helicoverpa zea* (Boddie) are among the main pests of maize. Both species exhibit cannibalistic behavior and quite often share the same feeding guild in maize (maize ears), which can result in several interspecific and intraspecific interactions. Paired interaction scenarios of intraspecific and interspecific larvae were assessed in arenas in the presence and absence of food to characterize movements resulting from interactions of these insects. There was a difference in the frequency of behavioral movements in all the interactions, except for *S. frugiperda* in the presence of food. Head touching and recoiling were the predominant movements in most of the interaction scenarios. *Spodoptera frugiperda* exhibited a predominance of defensive movements when competing against *H. zea* in the same instars. Cannibalism and predation occurred frequently in interactions involving 6th instar of *H. zea* against opponents in 4th instar. Larvae of *H. zea* show a higher aggressive movement than *S. frugiperda*. The larvae of *S. frugiperda* take advantage during the interactions, although they present more defensive movements compared to *H. zea*. This study provides relevant information regarding the interaction of these species and intraguild interaction, which might influence the population dynamics and the competitive displacement of pest species that share the same ecological niche.

Keywords Intraguild interaction · Ethogram · Fall armyworm · Corn earworm · Aggressive

Key message

- The intraguild interactions of fall armyworm and corn earworm are still unclear; moreover they exhibit cannibalistic/predation behavior and may share the same feeding niche in maize. Our studies have indicated the main movements in interactions between these species.
- Fall armyworm took advantage of corn earworm during the contests, although it presented more defensive movements.
- This is relevant information for population dynamics, displacement of species, and it has implications for transgenic maize insect resistance management strategies for these species.

Introduction

Helicoverpa zea (Boddie, 1850) (Lepidoptera: Noctuidae) and *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae) are among the most important pests of maize (*Zea mays* L.) in North and South America (Cruz et al. 1999; Burkness et al. 2015; Napal and Palacios 2015). Both insects exhibit cannibalistic behavior during the

Communicated by A. R. Horowitz.

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immature stages of their development (Pierce 1995; Chapman et al. 2000; Andow et al. 2015), which can occur mainly under low food availability and high population densities (Polis 1981; Elgar and Crespi 1992).

Cannibalism is an important factor in the population dynamics for several species (Alabi et al. 2009). This interaction can be responsible for 75 % of the mortality in *H. zea* populations, affecting population levels and temporal patterns of population peaks in maize (Stinner et al. 1977). In *S. frugiperda,* the cannibalistic behavior might occur at a frequency between 40 and 80 % when larvae are confined in groups (Chapman et al. 1999a, b).

Several aspects should be considered when examining cannibalism behavior. There are risks of injury or death by defense movements from conspecifics (Dawkins 1976; Polis 1981) and pathogens or parasites can be acquired through the consumption of infected conspecifics (Polis 1981); furthermore, instar specific predation can cause a reduction in inclusive fitness (Pfennig et al. 1993; Polis 1981). On the other hand, cannibalism might bring nutritional and energy benefits resulting in increased size, growth, and development of individuals (Eickwort 1973; Polis 1981; Elgar and Crespi 1992; Alabi et al. 2009). It can also result in indirect benefits by removal of a competitor (Fox 1975; Polis 1981) or by reducing the risk of predation (Chapman et al. 1999a, 2000).

In addition to cannibalism, intraguild predation may occur when different species share the same food source (Polis 1981; Wise 2006). This is the case involving the larvae of *S. frugiperda* and *H. zea* which occupy the same feeding guild in maize and often explore maize ears simultaneously (Burkness et al. 2010; Siebert et al. 2012), allowing possible interactions between the species. For *H. zea*, moths oviposit on maize silks, and larvae, as soon as hatch, they move on to feed on kernels (Burkness et al. 2010). Cannibalistic and carnivorous behavior, inclusive in interfamilial predation of *H. zea*, was reported in late instar larvae occupying the same maize ears (Capinera 2005; Boyd et al. 2008). Larvae of *S. frugiperda*, which are frequently related to attacks in the whorl stage plants (Cruz and Turpin 1983), may infest maize ears, similarly to *H. zea*, feeding on maize silk during the earlier stage of development, and moving and feeding on the developing kernels in advanced larval development (Pannuti et al. 2016).

Some studies have investigated the nutritional benefits and effects of cannibalism and intraguild predation on population dynamics, but there is still much to be clarified about the behavior of these larvae when the interspecific interactions occur (Dial and Adler 1990). Similarly, studies involving intraguild interactions among maize pests are fundamental to understand the larval movements and cannibalistic characteristics in the same guild (Dorhout and Rice 2010; Burkness et al. 2011). Moreover, the utilization of Bt transgenic crops in recent decades has changed the entomofauna of maize Lepidoptera (Horner and Dively 2003; Chilcutt 2006; Burkness et al. 2011). Insects which feed on Bt transgenic crops might be negatively affected during their development, and in consequence, be smaller than those that feed on non-Bt plants. This would lead to the consequence of the larval intraguild interaction (Horner and Dively 2003; Binning et al. 2014). The continuous release of hybrids expressing different endotoxins has also stimulated research on larval behavior.

Aggressive movements are very important for the acquisition of and/or defense of limited resources, allowing insects to survive and continue development and pass their genes to the next generations. Studies with the objective to evaluate cannibalism and intraguild predation of *H. zea* and *S. frugiperda*, as well as characterize attack and defense movements between these species will help clarify population fluctuations of both species and be useful for developing management strategies for each species in Bt and non-Bt maize crops.

In addition, the understanding of intraspecific and interspecific interactions will be useful to better understand how competitive displacement occurs between pest species sharing a given ecological niche, and consequently enhance integrated pest management strategies (Benelli 2015). This study has the objective to evaluate intraspecific and interspecific larval interaction between *S. frugiperda* and *H. zea* based on the characterization of offensive and defensive movements.

Materials and methods

Insects and plant material

Larval attack and defense movements of *S. frugiperda* and *H. zea* were characterized in interaction scenarios in the laboratory at the University of Nebraska, Entomology Department, Lincoln, NE, during 2014. Larvae of both noctuids were commercially acquired (Benzon Research Inc., Carlisle, PA, USA) and reared in plastic cups containing 15 mL of artificial diet (based on wheat diet developed by USDA, Stoneville, MS). Insects were kept in a growth chamber (25 ± 2 °C, 70 ± 10 % RH, 14:10 h (L:D)) until the appropriate instars were available to be used in the interaction scenarios.

Non-Bt maize seeds (hybrid Channel 208-71R) were sown in 5L pots with sterilized soil and fertilizer (34 % peat, 31 % perlite, 31 % vermiculite, and 4 % soil mix) in order to provide vegetative tissue for the scenarios that include food availability. Each pot held one maize plant and was maintained in a greenhouse free from pest infestation. The maize leaves were collected from plants at phenological stage V6 (Ritchie et al. 1993).

Ethogram bioassays

The ethogram bioassays were composed of five interaction scenarios involving combinations of larvae of *S. frugiperda* and *H. zea* (Table 1). Larvae (4–12 h after ecdysis) were taken separately from plastic cups with artificial diet and fasted for 2 h. The sex of the larvae was not determined because it does not effect the cannibalistic behavior, and developed larvae (4th to 6th instar) were utilized as the rates of cannibalism/predation and aggressive behavior are higher compared to earlier instars (Chapman et al. 1999b). For each bioassay replication, a pair of larvae was confined together on the opposite sides of Petri dishes (60 mm diameter × 15 mm height) with or without a maize leaf disk as food source, which was classified as food available or food not available. For treatments with food, in order to keep the maize tissue moist, two layers of solidified agar (2.5 % wt:vol, 2 and 1.5 mm thickness) were prepared in separate Petri dishes (60 by 15-mm Fisherbrand, Fisher, Pittsburgh, PA) according to methodology reported by Prasifka et al. (2007). For treatments without food, just the first layer of agar was positioned into the Petri dishes. Although maize leaves are not the preferential food of *H. zea*, the larvae can feed on maize leaves (Archer and Bynum 1994), and the objective of using leaf tissue was simply to analyze the behavior of the larvae in scenarios with and without a food source available.

Each scenario was recorded for 15 min to characterize larval interactions based on the larval movement. The movements were grouped in six categories (Table 2), comprising two attack movements and four defensive movements modified from previous studies (Dial and Adler 1990; Horner and Dively 2003). The camera used was a Dino-Lite AD413T-I2 V (Big C, Torrance, CA). Each larva participated only one time in a scenario, with a total of 30 pairs for each combination. Larval cannibalism or predation was also recorded after each interaction scenario.

Statistical analysis

A factorial arrangement (6 × 5) was used for analysis, with six characterized attack and defense movements and five interaction scenarios. Data were expressed as percentages of the total number of attack and defense movements exhibited in each interaction scenario, and analysis with or without food availability. Data were checked for normality and homogeneity of variances with Spearman correlation and Shapiro–Wilk test. The data were analyzed independently using Tukey test ($P \leq 0.05$) using the statistical program PROC MIXED-SAS 9.2 (SAS Institute 2001).

Results

S. frugiperda vs. *S. frugiperda* interaction scenarios

In the absence of food, we observed significant differences ($P < 0.0001$) among the attack and defense movements of *S. frugiperda* vs. *S. frugiperda* in all the scenarios assessed (Table 3). The most frequent movements were head touching and recoiling in 4th (vs. 4th), 5th (vs. 5th), and 6th

Table 1 Interaction scenarios of *Spodoptera frugiperda* and *Helicoverpa zea* with and without food

Without food	With food
S. frugiperda (4th) vs. *S. frugiperda* (4th)[a]	*S. frugiperda* (4th) vs. *S. frugiperda* (4th)
S. frugiperda (5th) vs. *S. frugiperda* (5th)[b]	*S. frugiperda* (5th) vs. *S. frugiperda* (5th)
S. frugiperda (6th) vs. *S. frugiperda* (6th)	*S. frugiperda* (6th) vs. *S. frugiperda* (6th)
S. frugiperda (4th) vs. *S. frugiperda* (6th)	*S. frugiperda* (4th) vs. *S. frugiperda* (6th)
S. frugiperda (6th) vs. *S. frugiperda* (4th)	*S. frugiperda* (6th) vs. *S. frugiperda* (4th)
H. zea (4th) vs. *H. zea* (4th)	*H. zea* (4th) vs. *H. zea* (4th)
H. zea (5th) vs. *H. zea* (5th)	*H. zea* (5th) vs. *H. zea* (5th)
H. zea (6th) vs. *H. zea* (6th)	*H. zea* (6th) vs. *H. zea* (6th)
H. zea (4th) vs. *H. zea* (6th)	*H. zea* (4th) vs. *H. zea* (6th)
H. zea (6th) vs. *H. zea* (4th)	*H. zea* (6th) vs. *H. zea* (4th)
H. zea (4th) vs. *S. frugiperda* (4th)[c]	*H. zea* (4th) vs. *S. frugiperda* (4th)
H. zea (5th) vs. *S. frugiperda* (5th)	*H. zea* (5th) vs. *S. frugiperda* (5th)
H. zea (6th) vs. *S. frugiperda* (6th)	*H. zea* (6th) vs. *S. frugiperda* (6th)
H. zea (4th) vs. *S. frugiperda* (6th)	*H. zea* (4th) vs. *S. frugiperda* (6th)
H. zea (6th) vs. *S. frugiperda* (4th)	*H. zea* (6th) vs. *S. frugiperda* (4th)

[a] Larval development: 4–12 h after ecdysis

[b] The first larvae listed in intraspecific scenario is the insect for which the observations were made

[c] In interspecific scenarios, movements were assessed for each species

Table 2 Attack and defense movements characterized in the interaction scenarios involving *Helicoverpa zea* and *Spodoptera frugiperda* (Adapted from Dial and Adler 1990; Horner and Dively 2003)

Interaction movements	Description
Attack	
Head touching	A sudden, rapid swing of the head and thorax to one or both sides, either across the opponent or the opponent's path; contact may or may not occur
Strike	A bite or jab with the head, directed toward the opponent, which may or may not contact the opponent
Defense	
Recoil	A single movement of part of the body, never directed toward the opponent, which does not displace the entire body
Wriggle	A rapid writhing of the entire body, without forward locomotion
Move away	a crawling away from the point of contact or dropping from the side of the arena after contact
Roll	A lateral flipping of the entire body while the legs and prolegs lose contact with the substrate

(vs. 6th), ranging from 1.17 to 3.38 times. In the scenario 4th instar (vs. 6th), the recoiling movement was the most frequent (Table 3). The most frequent movement for larvae in 6th (vs. 4th) was head touching. In general, striking, wriggling, and rolling were the least frequent larval movements. Head touching and recoiling were also the most frequent movements when the larvae were in 5th and 6th instars, with a head touching mean of 3.18 and 3.35 times, respectively, and a recoiling mean of 3.38 and 3.03 times, respectively.

With food available, larval movement only differed for larvae in 6th (vs. 6th), with a prevalence of head touching (8.47 times) and recoiling (8.08 times) ($P < 0.0001$), which were the most frequent compared to the other scenarios and similar to the movements observed in the absence of food (Table 3). Larva in 4th (vs. 6th) exhibited more attack movements in the presence of food and predominantly defense movements without food availability (Fig. 1).

Table 3 Mean numbers (±SE) of attack and defense movements of *Spodoptera frugiperda* against *Spodoptera frugiperda* with and without food availability

Movements	Instar of *Spodoptera frugiperda* (vs. instar of *Spodoptera frugiperda*)—without food					F^b	*df*	*P*
	4th (vs. 4th)[a]	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	1.17 ± 0.22aB	3.18 ± 0.58aA	3.35 ± 0.40aA	0.80 ± 0.43abB	1.37 ± 0.24aB	5.92**	20	<0.0001
Striking	0.15 ± 0.08bA	0.48 ± 0.14bA	0.73 ± 0.19bA	0.17 ± 0.11abA	0.13 ± 0.06bA			
Recoiling	1.23 ± 0.22aB	3.38 ± 0.66aA	3.03 ± 0.37aA	1.00 ± 0.20aB	0.77 ± 0.32abB			
Moving away	0.32 ± 0.08abA	0.85 ± 0.17bA	0.83 ± 0.15bA	0.77 ± 0.19abA	0.07 ± 0.07bA			
Wriggling	0.02 ± 0.02bA	0.05 ± 0.03bA	0.18 ± 0.09bA	0.47 ± 0.14abA	0.00 ± 0.00bA			
Rolling	0.00 ± 0.00bA	0.00 ± 0.00bA	0.02 ± 0.02bA	0.00 ± 0.00bA	0.00 ± 0.00bA			
	Instar of *Spodoptera frugiperda* (vs. Instar of *Spodoptera frugiperda*)—with food					*F*	*df*	*P*
	4th (vs. 4th)	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	0.38 ± 0.12 aB	0.57 ± 0.26aB	8.47 ± 1.20aA	0.23 ± 0.12aB	0.10 ± 0.05aB	26.51**	20	<0.0001
Striking	0.12 ± 0.07 aA	0.22 ± 0.11aA	1.02 ± 0.24bA	0.00 ± 0.00aA	0.00 ± 0.00aA			
Recoiling	0.42 ± 0.13 aB	0.60 ± 0.28aB	8.08 ± 1.20aA	0.10 ± 0.05aB	0.13 ± 0.10aB			
Moving away	0.18 ± 0.06 aA	0.13 ± 0.05aA	1.20 ± 0.24bA	0.07 ± 0.05aA	0.00 ± 0.00aA			
Wriggling	0.00 ± 0.00 aA	0.00 ± 0.00aA	0.20 ± 0.10bA	0.03 ± 0.03aA	0.00 ± 0.00aA			
Rolling	0.00 ± 0.00 aA	0.00 ± 0.00aA	0.00 ± 0.00bA	0.00 ± 0.00aA	0.00 ± 0.00aA			

Means followed by the same lower case letter in each column and uppercase letter in each row were not different, Tukey's HSD ($P > 0.05$)

** Difference among the treatments is highly significative

[a] Each condition (without and with food) was compared separately

[b] Values of *F*, *df*, and *P* related to the interaction in each condition

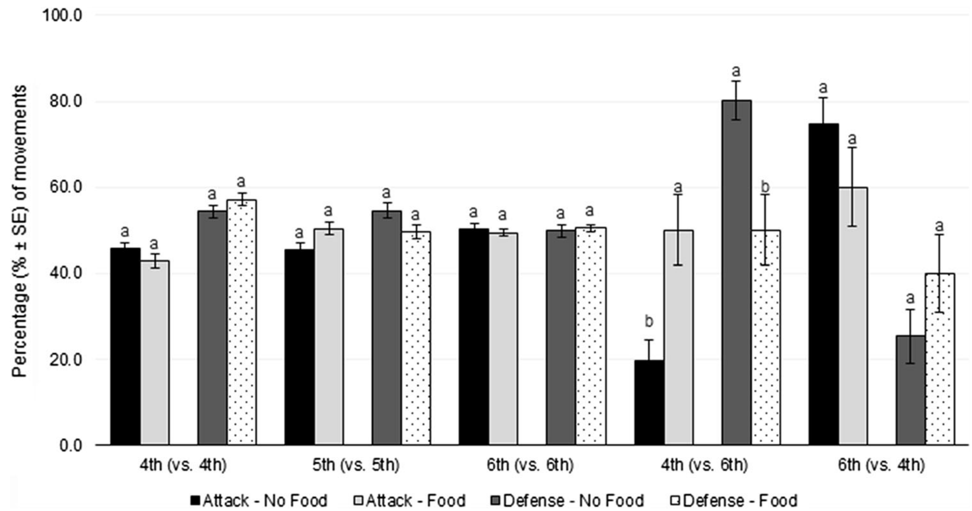

Fig. 1 Mean numbers (±SE) of attack and defense movements exhibited by *Spodoptera frugiperda* in intraspecific interaction in each scenario with and without food availability. *Mean bars* with the *same letter* are not significantly different ($P < 0.05$)

S. frugiperda vs. *H. zea* interaction scenarios

In the interaction scenario involving *S. frugiperda* vs. *H. zea* without food, the recoiling defensive movement was more frequent ($P < 0.0001$) than the other movements in 4th (vs. 4th), 5th (vs. 5th), and 6th (vs. 6th) (Table 4). No differences were detected in 4th (vs. 6th) and 6th (vs. 4th) scenarios, and the head touching movement was the dominant movement (1.47 times). Generally, wriggling and rolling movements were the least frequent movements displayed by the larvae. The head touching movement was most frequent when the larvae were in 6th instar (vs. larva of *H. zea* in 6th and 4th instar, with 1.93 and 1.47 times, respectively). Striking and recoiling were the predominant movement in 6th (vs. 6th) scenario. The moving away movement was most frequent in 5th larva (vs. 5th) and 6th (vs. 6th).

For *S. frugiperda* vs. *H. zea* scenario with food, the recoiling movement was again the most frequent in scenarios of 4th (vs. 4th), 5th (vs. 5th), 6th (vs. 6th), and 6th (vs. 4th) (Table 4). Moreover, wriggling and rolling movements continued to be the least frequent displayed by the *S. frugiperda*, except for scenario 4th (vs. 6th). Head touching, striking, and recoiling were dominant movements in 6th (vs. 6th). The larvae moved away less in 6th (vs. 4th) compared to 4th (vs. 4th), 5th (vs. 5th), and 6th (vs. 6th). The predominant attack movements of *S. frugiperda* in 6th vs. 6th scenario occurred under food available conditions, while the defense movements occurred when no food was available (Table 4; Fig. 2). In the absence of food, the defense movements were the most frequent movements. In scenarios of 4th (vs. 6th), the predominant movements were attack movements without food availability, and defense movements when food was available (Fig. 2).

H. zea vs. *H. zea* interaction scenarios

For the *H. zea* intraspecific interaction without food, the head touching movement (2.18) in 4th (vs. 4th) ($P < 0.0001$) was predominant (Table 5). Head touching and recoiling were the predominant movements in 5th (vs. 5th) and 6th (vs. 6th) interaction scenarios (ranging to 5.67–13.80 times). In general, the defensive wriggling and rolling movements were least frequent in these scenarios (from 0.03 to 2.73 times). With exception of the rolling, all other movements exhibited the high frequencies in scenario 6th (vs. 6th).

In the presence of food, the *H. zea* larvae of 4th, 5th, and 6th instars competing with larvae in the same age displayed more head touching and recoiling movement compared to the other movements, with values ranging from 1.52 to 5.15 times ($P < 0.0001$). In the scenario of 4th (vs. 6th), where the larvae displayed the highest defensive movement, recoiling and moving away were predominant (1.83 times for both). For the scenario 6th (vs. 4th), larvae displayed head touching as the predominant movement (2.26). With exception to the defense movements of rolling (with and without food) and wriggling (with food), the occurrence of movements was influenced by specific scenarios settings. In this case, the scenario 6th (vs. 6th) displayed the most frequent head touching, striking, recoiling, and moving away comparing with the other scenarios. Overall, the scenario 4th (vs. 4th) exhibited predominantly attack movements when no food was available and predominantly defensive movements when with food (Fig. 3).

H. zea vs. *S. frugiperda* interaction scenarios

In the scenario of *H. zea* vs *S. frugiperda* without food, the movements differed in the scenarios of 4th, 5th, and 6th

Table 4 Mean numbers (±SE) of attack and defense movements of *Spodoptera frugiperda* against *Helicoverpa zea* with and without food availability

Movements	Instar of *Spodoptera frugiperda* (vs. Instar of *Helicoverpa zea*)—without food					F^b	*df*	*P*
	4th (vs. 4th)[a]	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	0.68 ± 0.16bAB	1.23 ± 0.25bcAB	1.93 ± 0.42bA	0.17 ± 0.07aB	1.47 ± 0.30aA	19.45**	20	<0.0001
Striking	0.70 ± 0.18bB	1.07 ± 0.28bcAB	2.07 ± 0.52bA	0.33 ± 0.14aB	0.33 ± 0.11abB			
Recoiling	2.93 ± 0.49aC	4.77 ± 0.67aB	10.20 ± 1.13aA	0.93 ± 0.17aD	1.00 ± 0.15abD			
Moving away	0.83 ± 0.22bB	2.17 ± 0.34bA	2.63 ± 0.34aA	0.80 ± 0.19aB	0.07 ± 0.05bB			
Wriggling	0.03 ± 0.03bA	0.23 ± 0.09cA	0.27 ± 0.11cA	0.57 ± 0.11aA	0.00 ± 0.00bA			
Rolling	0.00 ± 0.00bA	0.00 ± 0.00cA	0.27 ± 0.09cA	0.00 ± 0.00aA	0.00 ± 0.00bA			
	Instar of *Spodoptera frugiperda* (vs. Instar of *Helicoverpa zea*)—with food					*F*	*df*	*P*
	4th (vs. 4th)	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	0.53 ± 0.17bcB	1.07 ± 0.31bcdB	3.60 ± 0.55bA	0.10 ± 0.05aB	0.83 ± 0.19abB	12.15**	20	<0.0001
Striking	0.33 ± 0.09cBC	1.33 ± 0.38bcAB	2.43 ± 0.45bcA	0.03 ± 0.03aC	0.30 ± 0.10bBC			
Recoiling	2.37 ± 0.37aC	3.73 ± 0.54aB	7.67 ± 0.84aA	1.20 ± 0.28aC	1.77 ± 0.41aC			
Moving away	1.77 ± 0.36abA	2.10 ± 0.47bA	1.57 ± 0.36cA	0.93 ± 0.25aAB	0.13 ± 0.06bB			
Wriggling	0.07 ± 0.05cA	0.10 ± 0.05cdA	0.10 ± 0.05dA	0.80 ± 0.13aA	0.03 ± 0.03bA			
Rolling	0.00 ± 0.00cA	0.00 ± 0.00dA	0.07 ± 0.05dA	0.00 ± 0.00aA	0.00 ± 0.00bA			

Means followed by the same lower case letter in each column and uppercase letter in each row were not different, Tukey's HSD ($P > 0.05$)

** Difference among the treatments is highly significative

[a] Each condition (without and with food) was compared separately

[b] Values of *F*, *df*, and *P* related to the interaction in each condition

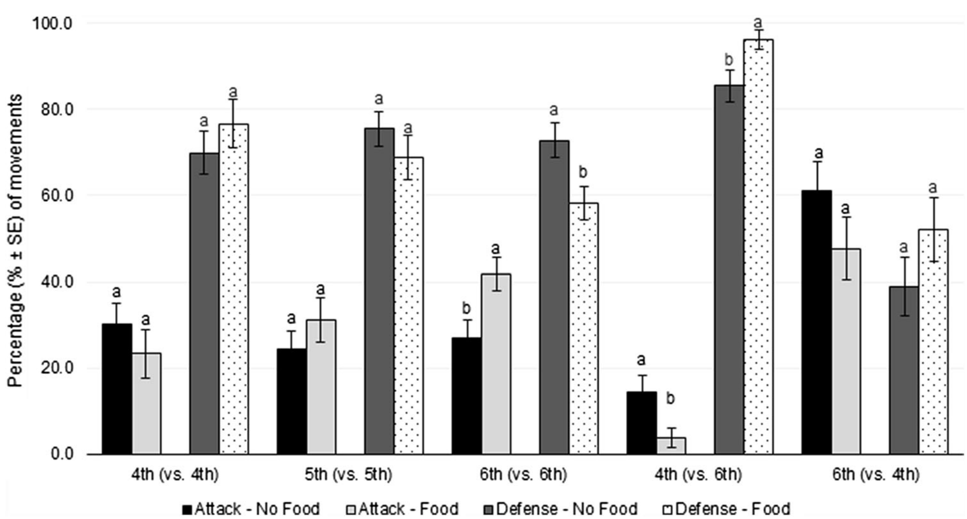

Fig. 2 Mean numbers (±SE) of attack and defense movements exhibited by *Spodoptera frugiperda* in interspecific interaction in each scenario with and without food availability. *Mean bars* with the *same letter* are not significantly different ($P < 0.05$)

instars against larvae in the same instar ($P < 0.0001$). The larvae more often displayed head touching attacks (3.70, 7.87, and 13.60 times, respectively) to the opponent (Table 6). In scenarios of 4th (vs. 6th) and 6th (vs. 4th), we did not observe differences among the movements. Regarding each movement, head touching was predominant in interaction scenarios involving *H. zea* larva in 6th instar (vs. 6th) (13.60 times), following by 5th (vs. 5th) scenario (7.87 times). Larvae also more often displayed striking and recoiling in the 6th (vs. 6th) scenario compared to 4th (vs. 6th).

In the presence of food, all scenarios more often exhibited head touching when compared to the other movements ($P < 0.0001$), ranging from 2.13 to 10.43 times (Table 5). Recoiling movements were also detected in 5th (vs. 5th) and 6th (vs. 6th) interaction scenarios (2.73 and 5.47 times,

Table 5 Mean numbers (±SE) of attack and defense movements of *Helicoverpa zea* against *Helicoverpa zea* with and without food availability

Movements	Instar of *Helicoverpa zea* (vs. Instar of *Helicoverpa zea*)—without food					F[b]	*df*	*P*
	4th (vs. 4th)[a]	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	2.18 ± 0.25aC	5.67 ± 0.39aB	13.80 ± 1.45aA	0.77 ± 0.19abC	2.03 ± 0.30aC	23.92**	20	<0.0001
Striking	0.63 ± 0.15abB	1.27 ± 0.32bcB	3.03 ± 0.32dA	0.33 ± 0.11abB	1.20 ± 0.23abB			
Recoiling	1.78 ± 0.16abC	5.78 ± 0.44aB	11.97 ± 1.27bA	1.03 ± 0.26abC	1.20 ± 0.22abC			
Moving away	1.08 ± 0.15abC	2.88 ± 0.30bB	7.03 ± 0.84cA	1.43 ± 0.28abBC	0.77 ± 0.20abC			
Wriggling	0.30 ± 0.08bBC	0.50 ± 0.08cBC	2.73 ± 0.49dA	1.90 ± 0.30aAB	0.03 ± 0.03bC			
Rolling	0.05 ± 0.03bA	0.03 ± 0.02cA	0.17 ± 0.07eA	0.07 ± 0.05bA	0.00 ± 0.00bA			
	Instar of *Helicoverpa zea* (vs. Instar of *Helicoverpa zea*)—with food					F	*df*	*P*
	4th (vs. 4th)	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	1.52 ± 0.24aB	1.73 ± 0.24aB	4.82 ± 0.34abA	0.57 ± 0.17bC	2.27 ± 0.29aB	12.70**	20	<0.0001
Striking	0.23 ± 0.06bcB	0.57 ± 0.14bcB	4.02 ± 0.56bcA	0.23 ± 0.10bB	0.70 ± 0.21bB			
Recoiling	1.65 ± 0.31aBC	1.90 ± 0.28aB	5.15 ± 0.41aA	1.83 ± 0.35aB	0.87 ± 0.21bC			
Moving away	1.12 ± 0.19abBC	1.30 ± 0.20abB	3.22 ± 0.21cA	1.83 ± 0.34aB	0.27 ± 0.10bC			
Wriggling	0.02 ± 0.02cA	0.28 ± 0.12cA	0.43 ± 0.11dA	0.87 ± 0.17bA	0.00 ± 0.00bA			
Rolling	0.00 ± 0.00cA	0.00 ± 0.00cA	0.43 ± 0.14dA	0.00 ± 0.00bA	0.00 ± 0.00bA			

Means followed by the same lower case letter in each column and uppercase letter in each row were not different, Tukey's HSD ($P > 0.05$)

** Difference among the treatments is highly significative

[a] Each condition (without and with food) was compared separately

[b] Values of F, *df*, and P related to the interaction in each condition

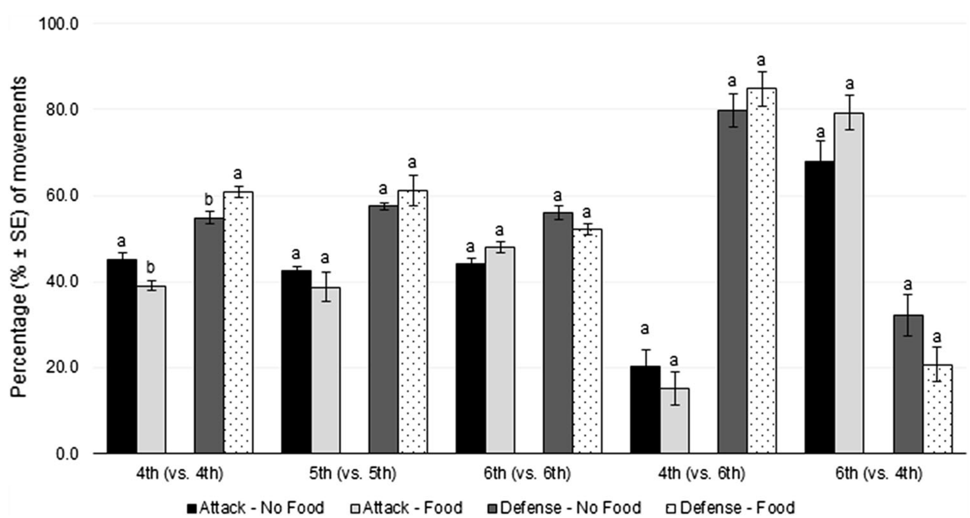

Fig. 3 Mean numbers (±SE) of attack and defense movements exhibited by *Helicoverpa zea* in intraspecific interaction in each scenario with and without food availability. *Mean bars* with the *same letter* are not significantly different ($P < 0.05$)

respectively). Overall, striking, wriggling, and rolling movements were least often displayed. The scenario 6th (vs. 6th) exhibited more frequent head touching, recoiling, and moving away movements compared to the other movements in other scenarios. Low frequency of these movements was detected in the scenarios involving larva in the 4th instar and 6th instar versus 4th. Comparing the movements of larva when food was available or without food available, *H. zea* larva in 6th instar exhibited a higher frequency of attack movements to 6th larva of *S. frugiperda* when no food was available. (Fig. 4). In scenarios 4th (vs. 6th) and 6th (vs. 4th), the *H. zea* larva exhibited more attack movements when food was available.

Cannibalism

Regarding the taxa cannibalism and predation in the scenarios with no food available, a difference was observed in

Table 6 Mean numbers (±SE) of attack and defense movements of *Helicoverpa zea* against *Spodoptera frugiperda* with and without food availability

Movements	Instar of *Helicoverpa zea* (vs. Instar of *Spodoptera frugiperda*)—without food					F^{b}	*df*	*P*
	4th (vs. 4th)[a]	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	3.70 ± 0.60aC	7.87 ± 1.27aB	13.60 ± 1.53aA	0.87 ± 0.20aD	1.47 ± 0.17aD	23.28**	20	<0.0001
Striking	0.28 ± 0.12bAB	0.33 ± 0.13cdAB	1.73 ± 0.44cA	0.00 ± 0.00aB	0.20 ± 0.07aAB			
Recoiling	1.67 ± 0.28bBC	3.27 ± 0.39bAB	4.07 ± 0.44bA	1.47 ± 0.16aC	1.07 ± 0.24aC			
Moving away	1.13 ± 0.19bA	1.73 ± 0.17bcA	1.23 ± 0.19cA	1.27 ± 0.17aA	0.53 ± 0.11aA			
Wriggling	0.05 ± 0.04bA	0.07 ± 0.05cdA	0.25 ± 0.12cA	0.67 ± 0.20aA	0.00 ± 0.00aA			
Rolling	0.00 ± 0.00bA	0.00 ± 0.00dA	0.03 ± 0.03cA	0.00 ± 0.00aA	0.00 ± 0.00aA			
	Instar of *Helicoverpa zea* (vs. Instar of *Spodoptera frugiperda*)—with food					*F*	*df*	*P*
	4th (vs. 4th)	5th (vs. 5th)	6th (vs. 6th)	4th (vs. 6th)	6th (vs. 4th)			
Head touching	2.67 ± 0.36aC	3.97 ± 0.60aB	10.43 ± 1.08aA	2.20 ± 0.43aC	2.13 ± 0.31aC	19.33**	20	<0.0001
Striking	0.07 ± 0.05bA	0.30 ± 0.15cA	0.67 ± 0.20dA	0.00 ± 0.00bA	0.33 ± 0.11bA			
Recoiling	1.07 ± 0.22bC	2.73 ± 0.49abB	5.47 ± 0.51bA	1.20 ± 0.22abC	0.27 ± 0.09bC			
Moving away	0.80 ± 0.15bBC	1.80 ± 0.35bAB	2.73 ± 0.33cA	1.17 ± 0.18abBC	0.20 ± 0.07bC			
Wriggling	0.00 ± 0.00bA	0.10 ± 0.05cA	0.33 ± 0.14dA	0.17 ± 0.10bA	0.00 ± 0.00bA			
Rolling	0.00 ± 0.00bA	0.00 ± 0.00cA	0.13 ± 0.10dA	0.00 ± 0.00bA	0.00 ± 0.00bA			

Means followed by the same lower case letter in each column and uppercase letter in each row were not different, Tukey's HSD ($P > 0.05$)

** Difference among the treatments is highly significative

[a] Each condition (without and with food) was compared separately

[b] Values of *F*, *df*, and *P* related to the interaction in each condition

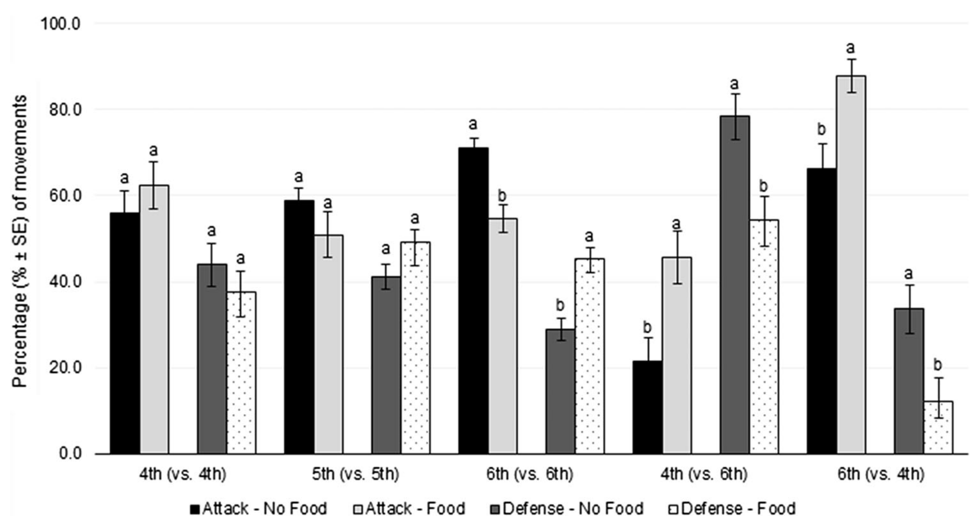

Fig. 4 Mean numbers (±SE) of attack and defense movements exhibited by *Helicoverpa zea* in interspecific interaction in each scenario with and without food availability. *Mean bars* with the *same letter* are not significantly different ($P < 0.05$)

S. frugiperda vs. *H zea*, in which the 6th instar preyed on the opponent in 13.3 % of the contests, and in *H. zea* vs. *H. zea* and *H. zea* vs. *S. frugiperda*, where the 6th instar cannibalized or preyed on the opponent in 53.3 and 46.7 % of the scenarios, respectively (Table 7). When food was available, *H. zea* competing with *H. zea* and *S. frugiperda* cannibalize or prey on the competitor in 56.7 and 53.3 % of the contests, respectively.

Discussion

In the intraspecific interaction scenario, both larva of *S. frugiperda* and *H. zea* exhibited head touching and recoiling as the prevalent movements when food was or was not available. The frequency of these movements increased with the development of the larvae, probably due to the high frequency of interactions when the larvae were

Table 7 Mean numbers (% ± SE) of cannibalism or predation in the scenarios of interaction with or without food availability during 15 min of contests

Scenarios	Cannibalism/predation (%)—without food			
	S. frugiperda vs. *S. frugiperda*[a]	*S. frugiperda* vs. *H. zea*	*H. zea* vs. *H. zea*	*H. zea* vs. *S. frugiperda*
4th vs. 4th	0.00 ± 0.00	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
5th vs. 5th	0.00 ± 0.00	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
6th vs. 6th	0.00 ± 0.00	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
4th vs. 6th	0.00 ± 0.00	0.00 ± 0.00b	0.00 ± 0.00b	0.00 ± 0.00b
6th vs. 4th	3.33 ± 3.28	13.33 ± 6.21a	53.33 ± 9.11a	46.67 ± 9.11a
F	8.87	16.33**	55.56**	30.84**
df	4, 145	4, 145	4, 145	4, 145
P	0.0921	<0.0001	<0.0001	<0.0001
Scenarios	**Cannibalism/predation (%)—with food**			
	S. frugiperda vs. *S. frugiperda*	*S. frugiperda* vs. *H. zea*	*H. zea* vs. *H. zea*	*H. zea* vs. *S. frugiperda*
4th vs. 4th	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00b	0.00 ± 0.00b
5th vs. 5th	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00b	0.00 ± 0.00b
6th vs. 6th	0.00 ± 0.00	3.33 ± 3.28	0.00 ± 0.00b	0.00 ± 0.00b
4th vs. 6th	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00b	0.00 ± 0.00b
6th vs. 4th	0.00 ± 0.00	3.33 ± 3.28	56.67 ± 9.05a	53.33 ± 9.11a
F	41.48	9.61	35.61**	30.88**
df	4, 145	4, 145	4, 145	4, 145
P	–	0.3291	<0.0001	<0.0001

Means followed by the same letter in each column were not different, Tukey's HSD ($P > 0.05$)

** Difference among the treatments is highly significative

[a] Each condition (without and with food) was compared separately

bigger and more mobile compared to the smaller larvae. However, when the larvae were in interspecific interaction scenarios, the predominant movement of *S. frugiperda* was defense recoiling, while *H. zea* exhibited a higher frequency of attack movements. These results suggest that when these species interact, *S. frugiperda* tends to be less aggressive than *H. zea*, trying to defend from *H. zea* attack movements more than initiate attacks. The highest frequency of attack movement in the scenarios of 6th vs. 6th is also likely linked to the larger size of the larvae and higher mobility than that of earlier instars. Moreover, the interactions between larger larvae were more aggressive than the others, and although they did not exhibit cannibalism during this interaction, the injuries to the larvae were noticeable. Future studies should be conducted in field conditions in order to check the movements of larvae in natural conditions, where the larval behavior might be influenced by variable abiotic conditions and presence of predators.

As expected, larval age is an important factor in intraspecific and interspecific interactions. Larvae of 6th instar against 4th always had advantages in the contests between the species studied. Based on some animal behavior studies, the success of fighting is directly dependent on physical disparities like size, strength, and weaponry (Dodson 1986; Shelly 1999; Briffa 2008; Arnott and Elwood 2009), and the presence of resources, physical exertion, and experience in previous fights (Brown et al. 2006; Stevenson and Schildberger 2013).

The later lepidopteran instars often exhibit a greater tendency to engage in cannibalism compared with their younger conspecifics, mainly when larvae of different stages are enclosed together (Chapman et al. 1999a, b). In this study, larvae of 4th instar of *H. zea* and *S. frugiperda* exhibited similar movements against the larvae of 6th instar in intraspecific and interspecific interactions, with a low frequency of movements. Furthermore, although distances between larvae and their velocity during each movement were not evaluated in this study, it was observed that both species try to keep a safe distance from the bigger competitor, and *H. zea* appears to be faster than *S. frugiperda* when trying to escape after an encounter, thus avoiding the predation or cannibalism. The faster movement of *H. zea* after an interaction was also observed in the other scenarios. In a situation where the superficial area is larger than the arena used in this study, and the larva has high velocity movement, then it will likely have a greater probability to escape from cannibalism or predation. It is possible that in a maize ear, which represents an arena with confined conditions, cannibalism and predation might be more frequent (Dial and Adler 1990), and larval velocity would continue to be an important factor for these contests. Future research should be conducted in order to evaluate more specific parameters, such as distance between larvae, distance moved, and velocity, which might add to the understanding of the different movements observed between the species evaluated in this study.

Regarding *H. zea*, the frequent larval movement and predominant attack movements in 6th instar were also reported in other intraspecific interaction studies (Dial and Adler 1990). The aggressive movements were related to larval cannibalism (Gould et al. 1980), which increase in the late larval instar of *H. zea*, when it colonizes maize ears (Capinera 2005). Among the occurrence of cannibalism and predation, contests involving 6th instar of *H. zea* often resulted in mortality of the opponent when it was in 4th instar, proving the importance of larval development on a maize ear. In addition, aggressiveness of *H. zea* does not change if the interaction was in intraspecific or interspecific interactions, which indicate that this behavior is not regulated by different competitor species of same feeding guild. For other species of *Helicoverpa*, larvae of *Helicoverpa armigera* (Hubner, 1805) (Lepidoptera: Noctuidae) are more aggressive than *Helicoverpa punctigera* (Wallengren, 1860) (Lepidoptera: Noctuidae), and consequently, cannibalism rates are higher in *H. armigera* than in the other species (Fox 1975).

Besides the species involved in the study, the availability of a food source can influence the behavior of larvae. In this study, the predominant attack movements (food available) in intraspecific interaction of *S. frugiperda* in 4th vs. 6th instar and *H. zea* 4th instar vs. *S. frugiperda* 6th instar might have occurred because the larger larvae prioritized the feeding time at the source of food, decreasing the chances to cannibalize or prey on the smaller competitor. In scenario of 4th vs. 4th instar of *H. zea* (intraspecific) and 6th vs. 6th instar of *H. zea* against *S. frugiperda*, the predominant attack movements of *H. zea* in the absence of food is evidence of the importance of food availability for intraguild interaction, and suggests that the larval interactions might increase when food is less available.

The quality and attractiveness of the food source is another important factor that might cause modifications in larval behavior. Studies involving Bt maize indicated that *H. zea* reduces the frequency of cannibalism and aggressiveness behaviors in uneven instar intraspecific interactions when the larvae were fed on MON810 (Cry1Ab) Bt maize, which can provokes a suppression in the population (Horner and Dively 2003). Under field conditions, researchers reported greater larval survival in Bt maize ears compared to non-Bt maize ears, also suggesting the reduction of aggressiveness in this condition (Horner et al. 2003). Other studies involving cannibalism and intraguild predation of this species in the presence of Bt protein (Cry1Ab) in maize indicated reduced survival of *H. zea* in late instars on Bt maize, which decreases the regular rates of cannibalism and the *H. zea* – *S. frugiperda* intraguild predation of late instars on early instars. A reduction in cannibalistic behavior of *H. zea* might increase the survival of larvae in multiple infestations of Bt maize ears (Chilcutt et al. 2007). Negative effects of Cry1Ab protein in *H. zea* behavior were also observed in an intraguild interaction study involving this species, *Striacosta albicosta* (Smith) (Lepidoptera: Noctuidae), and *Ostrinia nubilalis* (Hübner) (Lepidoptera: Noctuidae) (Dorhout and Rice 2010). On the other hand, other studies indicated that cannibalism of *H. zea* increased when larvae fed on Cry1Ab Bt maize in comparison with larvae reared on non-Bt maize (Chilcutt 2006). Regarding *S. frugiperda*, the occurrence of resistant populations of this species to Cry1F in Brazil (Farias et al. 2015) emphasizes the importance of the food source for both species and raises questions about the influence of this on the larval behavior during intraguild interaction.

Larvae of *S. frugiperda* exhibited less aggressive movements than *H. zea.* Although cannibalism in *S. frugiperda,* under field and laboratory conditions is well documented (Chapman et al. 1999a, b; Sarmento et al. 2002; Chapman et al. 2000; Goussain et al. 2002), recent studies indicated that this behavior may not occur frequently (Da Silva and Parra 2013; Bentivenha et al. 2016), which might support observations of *S. frugiperda*'s lower level of aggressiveness compared to *H. zea*. Although the lower aggressiveness of *S. frugiperda* and its seemingly lower mobility suggest vulnerability and disadvantage when interactive with *H. zea*, intraguild studies has showed that this species can gain advantage in interaction against *H. zea*. This advantage probably occurs because of the higher survival of *S. frugiperda* compared to *H. zea*, when competing on a non-Bt maize ear in different interaction scenarios (Bentivenha et al. 2016). This higher survival of *S. frugiperda* might be related to the better skills of this species in attack or defense during the contests, or movements such as a counter attack. Although larvae of *H. zea* frequently were the first to present an attack movement, *S. frugiperda* rarely quit the contests, while *H. zea* frequently quit the contest after the first attack. Moreover, this advantage might be related to some larvae morphological characteristic, such as integument or mandible architecture, since even when they were in the same instar; therefore *S. frugiperda* gained an advantage against *H. zea* in the intraguild scenarios.

Another relevant factor for this interaction may be related to the earlier occurrence of *S. frugiperda* in maize. Larvae of this species occur earlier on maize plants, during the vegetative stage of the plant, moving to the maize ear when the plants reach the reproductive stage (Pannuti et al. 2016). This factor would allow larvae of *S. frugiperda* to infest the maize ear without the competition with larvae of *H. zea*. Thus, when larvae of *H. zea* start to infest a maize crop, there would be a higher possibility to encounter larvae of *S. frugiperda* in a more advanced stage of development inside a maize ear, favoring the bigger ones in a possible interaction. In case the maize ear is not previously colonized by *S. frugiperda*, the first larva of *H. zea* to reach the structure could be favored and predate the later arriving larvae (Kirkpatrick 1957), since size and position are important factors for cannibalism (Dial and Adler 1990). Otherwise, if the larva is in a molting stage, it is less aggressive and its mobility is decreased, so an intermolting larva is vulnerable to be predated or cannibalized (Dial and Adler 1990). In addition, both species might pass through more than one generation in maize (Cruz and Turpin 1983; Cunningham and Zalucki 2014), and might cohabit in other important crops, such as soybean and cotton (Hardwick 1965; Barros et al. 2010; Malaquias et al. 2015), which increases the importance of host plant as a relevant factor for infestation, prevalence, and interaction of the species.

Under ethogram recording, cannibalism or predation occurs only during contests between 6th and 4th instar and 6th and 6th instar (although no difference was observed in this scenario compared to others). Even without cannibalism or predation, the presence of injuries caused by larval attacks could result in the failure of ecdysis because of the high internal pressure during molting and possible loss of hemolymph (Reynolds 1980). Recent studies conducted with *H. armigera* demonstrated that larvae that had excessive cannibalistic behavior decreased their fitness, resulting in small body size, and delay of larval development (Kakimoto et al. 2003). For *S. frugiperda,* the cannibalistic behavior resulted in a reduction of larval survival, even with food available, and lower pupal weight and a reduced development rate when under low food quality conditions (Chapman et al. 1999b). According to the research, cannibalism in *S. frugiperda* might be an indirect advantage through the elimination of competitors (Chapman et al. 2000). The reasons under which a larva cannibalizes or preys on a competitor might be related to obtaining a high nutritional value meal in an environment of low nutritional value food, like when only maize leaves are available (Da Silva and Parra 2013). Even with food abundance, cannibalism might occur and could be directly affected by density of insects (Polis 1981). Furthermore, cannibalism seems to be an adaptive behavior for larger larvae, because this behavior is more often in pairs of different instar classes. Frequently, small larvae of *H. armigera* are cannibalized by large larvae, and due to this, larvae tend to escape if the competitor is larger in size, or fight if the competitor is smaller, which suggests an adaptive behavior (Kakimoto et al. 2003).

A knowledge of aggressive and defensive movements among pests who share the same guild is valuable information for IPM (Benelli 2015). The understanding of intraspecific and interspecific interaction is necessary to better understand how these contests might affect population dynamics and competitive displacement of pest species that share a given ecological niche. This study contributed to understanding the behavioral movements and the intraguild interactions of two of the most important maize pests in North America. Additional field studies involving non-Bt and Bt maize should be conducted in order to verify the prevalence of these species when competing with different food sources (resistant/susceptible) in the same feeding guild. Further research on lepidopteran behavior is needed in order to clarify the importance of this interaction for the population dynamics, life history, survival on non-Bt and Bt maize, cross-pollinated maize ears, and consequently, for resistance management strategies within IPM.

Author contribution statement

All authors conceived and designed research. JPGFS and DGM conducted experiments. All authors analyzed data. JPGFS wrote the manuscript. All authors read, edit, and approved the manuscript.

Acknowledgments We thank Ana Maria Velez and James Kalisch (University of Nebraska) for the technical support.

Funding Funding for research was provided by the Coordination for the Improvement of Higher Education Personnel (99999.002564/2014-09).

Compliance with ethical standards

Conflict of Interest All authors declare that they have no conflict of interest.

Ethical Approval This article does not contain any studies with human or animal performed by any of the authors.

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