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## Larval dispersal of the invasive fall armyworm, *Spodoptera frugiperda*, the exotic stemborer *Chilo partellus*, and indigenous maize stemborers in Africa

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### Abstract

Larval dispersal either through ballooning or crawling results in a redistribution of the insect population and infestations within and between plants. In addition, invasive species, such as the fall armyworm (FAW), *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), and the exotic stemborer *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae), may displace indigenous stemborers on maize in Africa. To test whether larval dispersal activity may play a role in the displacement of indigenous stemborers, larval dispersal was compared between FAW, *C. partellus*, and the indigenous species *Busseola fusca* (Fuller) and *Sesamia calamistis* (Hampson) (both Lepidoptera: Noctuidae). Twenty potted maize plants were infested with one batch of eggs either from stemborers (*B. fusca*, *S. calamistis*, or *C. partellus*) or from FAW and monitored in the greenhouse for ballooning activities. After egg hatching, both ballooning and non-ballooning larvae were identified according to species and counted. FAW neonate larvae had greater potential for ballooning off than stemborers, irrespective of species. For each species, more females dispersed than males, and their survival rate was higher than that of non-ballooning larvae. In addition, plant-to-plant larval movements were studied using 6.25-m<sup>2</sup> plots of caged maize in a completely randomized design with five replicates. FAW was found to have wider dispersal and plant damage potential than any of the stemborer species. In conclusion, in contrast to *C. partellus*, the invasive characteristic of FAW can be explained, in part, by its higher larval dispersal activity compared to stemborers. This difference in larval dispersal might also be considered in sampling plans for monitoring pest density in the field.

### Introduction

Insect dispersal is an important form of adaptation to ensure survival in an environment with variable resources and habitats (Bello, 1990; Price, 1997; Pannuti et al., 2016). Most studies have focused on flight as a means of dispersal (e.g., Landin, 1980; Osborne et al., 2002; Wyckhuys & O'Neil, 2006). Other means of spreading involve larvae crawling or ballooning off (Zalucki et al., 2002;

Pannuti et al., 2015, 2016; Rojas et al., 2018). However, much less is known about their significance as a means of dispersal.

Larval dispersal is common among species that lay eggs in batches, such as lepidopterans (Zalucki et al., 2002; Meagher & Nagoshi, 2004; Tiple et al., 2011). Adaptive dispersal enables larvae to switch feeding sites and to move from impoverished food resources to new ones. It also allows the larvae to escape enemies and to change location within the plant (Pannuti et al., 2016). The larvae migrate from the oviposition plant to adjacent plants either as ballooning larvae or as crawling older larvae (Zalucki et al., 2002; Schoonhoven et al., 2005). Ballooning larvae can migrate to other plants with the silk strand still attached to

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the original leaf. Sometimes several larvae spin off in a row, hanging onto the same thread. They may also spin off, and either continue on or climb back to the original plant (Zalucki et al., 2002; Schoonhoven et al., 2005).

In sub-Saharan Africa, the stemborers *Busseola fusca* (Fuller), *Sesamia calamistis* (Hampson) (both Lepidoptera: Noctuidae), and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) are the economically most important lepidopteran pest species, severely limiting the yield of maize as they continuously infest the crop throughout its growth stages (Kfir et al., 2002; Oben et al., 2015). They may occur as single species or as a community of mixed species (Van Den Berg et al., 1991; Tefera, 2004; Ong'amo et al., 2006; Krüger et al., 2008). Among these stemborers, *C. partellus* is the only exotic species which invaded eastern Africa in the 1930s (Kfir et al., 2002). This species has competitively displaced *B. fusca* in the highlands of South Africa (Kfir, 1997). It has also displaced *Chilo orichalcociliellus* Strand in the coastal region of Kenya (Ofomata et al., 1999) and may gain an advantage over *B. fusca* and *S. calamistis* in the utilization of maize (Mwalusepo et al., 2015; Ntiri et al., 2016). Recently, the fall armyworm (FAW), *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), invaded sub-Saharan Africa, where it has seriously limited maize yields (Goergen et al., 2016; Cock et al., 2017; Fotso Kuate et al., 2019). Recent observations indicate that it closely interacts with maize stemborer communities (Sokame et al., 2020) and might also displace the stemborers. Among these species, the females of *B. fusca* and *S. calamistis* lay their eggs between the leaf sheath and the stem of the plant, protected against environmental influences and natural enemies, whereas *C. partellus* and *S. frugiperda* deposit eggs directly on leaf surfaces, which makes them disperse faster and more efficiently between plants (Pitre et al., 1983; Polaszek, 1998). The latter might explain their invasive characteristics compared to indigenous pests.

In this context, larval dispersal by means of ballooning off and crawling was compared between FAW, *C. partellus*, and indigenous stemborers. In addition, the consequences of ballooning off on fitness parameters, such as larval and pupal survival, as well as development time and sex ratio, were determined. As several studies showed that stemborers and FAW display aggregative behavior in maize fields not far from the original oviposition site (Van Rensburg et al., 1987; Ross & Ostlie, 1990; Van Den Berg et al., 1991; Calatayud et al., 2014; Erasmus et al., 2016; Ndjomatchoua et al., 2016; Pannuti et al., 2016), the movements of larvae by both ballooning off and crawling between adjacent plants and the plant damage inflicted were studied in small cages.

## Materials and methods

### Plants and insects

All experiments were carried out at the Duduville campus of the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya. Maize plants used were hybrid H513 (Simlaw Seeds, Nairobi, Kenya). For the ballooning off experiment, plants were grown in plastic pots containing peat (12 cm high, 13 cm diameter, with a single maize plant per pot) in a greenhouse, whereas for the plant-to-plant movement experiment, plants were grown directly in soil covered with a netted cage of 2.5 × 2.5 m at the *icipe* Duduville campus. Mean temperatures were approximately 31 °C in the day and 17 °C in the night, with a L12:D12 photoperiod. Plants aged between 4–6 weeks and 60–75 cm high were used for all experiments. This age was found to be the plant's growth stage used by both stemborers and FAW females for oviposition (Holloway, 1998; Polaszek, 1998; Goergen et al., 2016; Cock et al., 2017).

The pupae of *B. fusca*, *C. partellus*, *S. calamistis*, and *S. frugiperda* were obtained from colonies reared at the Animal Rearing and Containment Unit (ARCU) at *icipe*, Nairobi, Kenya. Colonies were rejuvenated twice a year with field-collected larvae. Pupae were sexed, and males and females were kept separately in plastic containers (21 × 15 × 8 cm) until adult emergence. A cotton pad moistened with water was placed inside the container to maintain relative humidity >80%. The insects were kept in a rearing room at 25 ± 0.05 °C, 58.5 ± 0.4% r.h., and L12:D12 photoperiod.

For each species, emerged adult males and females were released in a mating cage (40 × 40 × 63 cm), at the onset of the scotophase. The mating status was checked at hourly intervals until the end of the scotophase. Pairs of mating moths were collected in plastic jars (8 cm high, 5 cm diameter). From these pairs, the gravid females were individually released in the aforementioned mating cages the following night, with each containing one potted maize plant. Egg deposition was checked the following day. For each species, each potted plant with one batch of eggs containing a similar number of eggs per batch was used in the following two experiments.

### Ballooning activity

For each species, 20 potted maize plants with one egg batch each were placed in the greenhouse at 26 ± 2.5 °C and 65–70% r.h. The potted plants were placed 1 m apart to avoid leaf overlap from different plants. Five (*B. fusca* and *S. calamistis*) or 3 days (*C. partellus* and *S. frugiperda*) after oviposition, the plants were checked early each day for hatching eggs. At eclosion, the newly hatched larvae were observed for ballooning activity every 5–10 min during

the 1st h, and every 20 min during the 2nd and 3rd h. All larvae that left the maize plants by hanging on silk threads were collected and individually put on an artificial diet in a glass vial (7.5 × 2.5 cm). After 3 h, the experiments were stopped, when most of the larvae had entered the plant via the whorl or leaf sheath or had left the plant on silk threads. The plants were dissected, and the non-ballooning larvae were recorded from each plant. The egg batch was removed from the dissected plant, and the total number of eggs (hatched or not) on each plant was recorded in order to estimate the egg-hatching rate. The larvae found on the ground around each potted plant were removed and were considered as having left or dropped off the plant without spinning off. These larvae, in addition to dead larvae, which were not collected, were not taken into account in the analysis and were very few in number, representing only (mean ± SE, n = 20) 3.83 ± 0.71% for *B. fusca*, 4.50 ± 0.87% for *S. calamistis*, 3.37 ± 0.58% for *C. partellus*, and 9.27 ± 1.01% for FAW of the total collected larvae from the total eggs hatched.

For each egg batch and species, ballooning and non-ballooning larvae were kept separately on artificial diet in the laboratory rearing room (at 25 ± 2 °C, 60 ± 10% r.h., and L12:D12 photoperiod) until pupation to estimate larval development time. Pupae were sexed according to the method described by Underwood (1994). They were kept in separate plastic containers (16 × 10 cm) with perforated plastic lids until adult emergence to estimate pupal development time. Larval or pupal survival for each species was calculated by dividing the number of larvae that pupated or pupae that emerged by the number of the total larvae or pupae recorded for a given species, respectively.

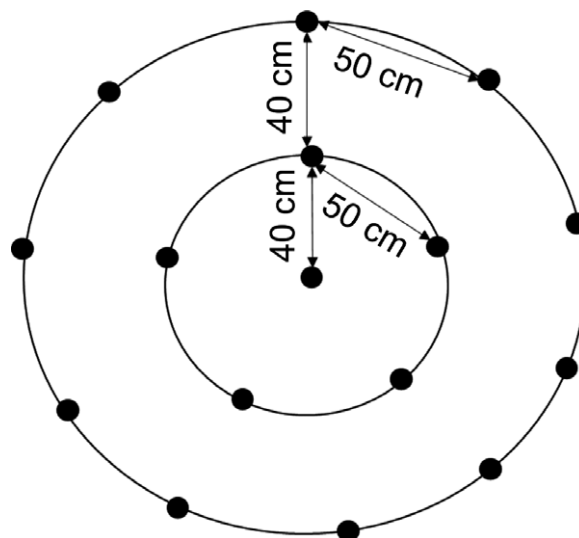
#### Larval movement between adjacent plants via ballooning or crawling off

The study was conducted with a completely randomized design. For each species, there were five replicates, each consisting of a caged 6.25-m<sup>2</sup> plot in the *icipe* campus field. Thermo-photoperiod was approximately L12(31 °C):D12 (17 °C). Each cage was 2.5 m wide, 2.5 m long, and 2 m high, supported with polyvinyl chloride (PVC) pipes (3 cm diameter) and covered with a white insect net (mesh 16, or holes of 1.19 mm). Maize was planted directly in the soil in the *icipe* campus field in two concentric circles, as shown in Figure 1. Two seeds were planted per hole but reduced to one plant 1 week after germination. Following the results from dispersal of stemborer and FAW larvae by Erasmus et al. (2016), Ndjomatchoua et al. (2016), Pannuti et al. (2016), Ross & Ostlie (1990), Van Den Berg et al. (1991), and Van Rensburg et al. (1987), two concentric circles with a radius of 40 and 80 cm were chosen (Figure 1). The plots were irrigated as required

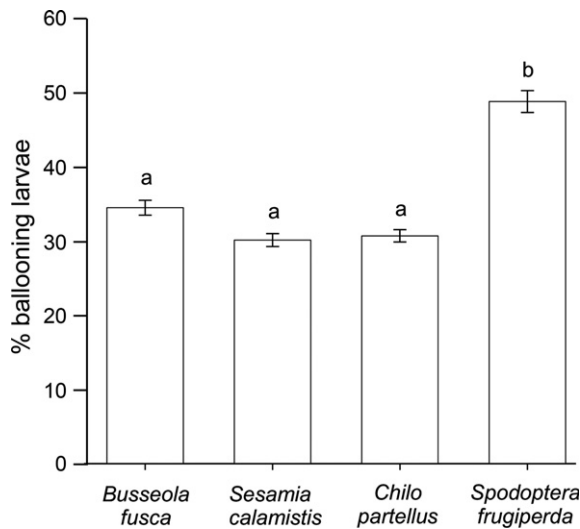
with a lateral overhead irrigation system. When the plants were 4–6 weeks old (the same age as described above for the potted plants), one potted maize plant with one egg batch obtained as described above was placed in the centre of the circles. After 1 week, the egg batch was removed from the plant, all eggs (hatched and non-hatched) were counted under a stereo microscope, and the hatching rate was calculated. Three weeks later, each plant was assessed for leaf damage and larval density. Leaf damage was evaluated using the damage scale described by Prasad et al. (2011): 1 = no visible leaf injury or a small number of pin/shot-hole types of injury on a few leaves; 2 = small amount of shot-hole type lesions on a few leaves; 3 = shot-hole type injury on several leaves; 4 = several leaves with shot-holes and elongated lesions; 5 = several leaves with elongated lesions of ca. 2.5 cm; 6 = several leaves with elongated lesions of >2.5 cm; 7 = long lesions on about half of the leaves; 8 = long lesions on about two-thirds of the leaves; and 9 = most leaves with long lesions based on the type and amount of feeding. Infestation incidence was expressed as the percentage of plants damaged in each plot. Finally, the plants were uprooted and dissected to estimate larval density per plant.

#### Data analysis

The proportion of ballooning larvae, sex ratio, survival rate, hatching rate, and infestation incidence were analyzed with a generalized linear model (GLM) with the binomial error distribution due to the binary nature of these



**Figure 1** Crop geometric of the maize plot. The central dot represents the initial point of infestation in the plot. Five maize plants were planted in an inner circle with 40 cm radius and 10 maize plants in an outer circle with 80 cm radius from the initial point of infestation.



**Figure 2** Mean ( $\pm$  SE) percentage of larvae of fall armyworm (*Spodoptera frugiperda*) and three stemborer species leaving maize plants by ballooning. Means capped with different letters are significantly different (Tukey's test:  $P < 0.05$ ).

parameters (ballooning vs. non-ballooning, female vs. male, survival vs. mortality, hatched vs. non-hatched, and infested vs. uninfested) (Warton & Hui, 2011). Larval and pupal development time and the number of eggs per batch were analyzed with GLM with the Poisson error distribution, whereas the number of larvae per plant and leaf damage scoring were analyzed with GLM with a negative binomial error distribution due to the nature of the count data and the goodness of fit model. Means were separated with Tukey's multiple comparison tests, performed in the R package 'lsmeans' (Lenth, 2016). FAW and the stemborer species were taken as explicative variables in addition to the distance from the point of infestation in the between-plant dispersal experiment. All analyses were carried out in R v.3.5.1 (R Core Team, 2018) and  $\alpha = 0.05$ .

## Results

### Numbers of eggs per batch and eggs hatching rates of FAW and maize stemborers

The mean ( $\pm$  SE;  $n = 25$ ) number of eggs per batch obtained in this study was  $64.6 \pm 4.1$  for *B. fusca*,  $60.1 \pm 4.6$  for *S. calamistis*,  $59.4 \pm 4.4$  for *C. partellus*, and  $63.1 \pm 4.0$  for FAW with hatching rates of  $91 \pm 1.6$ ,  $95 \pm 0.83$ ,  $95 \pm 0.64$ , and  $92 \pm 0.89\%$ , respectively. Between species, the number of eggs per batch and the number of eggs hatched per batch were not significantly different (GLM: LR = 7.42,  $P = 0.06$ ; LR = 2.72,  $P = 0.43$ , respectively). Therefore, the number of eggs per batch and egg-hatching rate were not the factors which

could influence all larval movements evaluated in this study.

### Ballooning activity

The three stemborers exhibited similar ballooning rates but they were lower than those of FAW (LR = 99.69,  $P < 0.0001$ ; Figure 2). About 50% of the FAW larvae ballooned off the plant compared with only 30% of the stemborers.

For either ballooning or non-ballooning larvae, there was no significant difference of larval and pupal survival between species (Table 1). However, within each species, the larvae and pupae coming from ballooning larvae exhibited higher survival rates as compared to those from non-ballooning larvae. For the development time of both larvae and pupae, there was no significant difference between ballooning and non-ballooning larvae regardless of the pest species. However, for both ballooning and non-ballooning FAW larvae development time was shorter than in the stemborer species (Table 1).

Regardless of the species, the ballooning larvae that pupated produced a higher percentage of females than the non-ballooning larvae (*B. fusca*: LR = 124.6; *S. calamistis*: LR = 17.2; *C. partellus*: LR = 16.1; FAW: LR = 25.4, all  $P < 0.0001$ ; Figure 3). However, there were no differences for ballooning (LR = 0.43,  $P = 0.93$ ) and non-ballooning (LR = 0.10,  $P = 0.99$ ) larvae between insect species (Figure 3).

### Larval movement between plants

Fall armyworm had a significantly higher number of plants infested and larvae per plant than the stemborer species (Table 2). In contrast to FAW, infestation incidence and number of larvae in the three stemborers were higher at 40 cm than at 80 cm (GLM; infestation incidence, *B. fusca*: LR = 7.78,  $P = 0.03$ ; *S. calamistis*: LR = 4.10,  $P = 0.04$ ; *C. partellus*: LR = 3.26,  $P = 0.04$ ; FAW: LR = 0.24,  $P = 0.62$ ; number of larvae per plant, *B. fusca*: LR = 8.02,  $P = 0.004$ ; *S. calamistis*: LR = 6.48,  $P = 0.01$ ; *C. partellus*: LR = 5.09,  $P = 0.02$ ; FAW: LR = 2.00,  $P = 0.15$ ).

The damage rating scale decreased with the distance from the initial point of infestation for the stemborer species but not for FAW (*B. fusca*: LR = 4.75,  $P = 0.02$ ; *S. calamistis*: LR = 4.16,  $P = 0.03$ ; *C. partellus*: LR = 6.32,  $P = 0.01$ ; FAW: LR = 1.87,  $P = 0.17$ ). Damage ratings were lower for stemborers than for FAW (LR = 11.78 at 40 cm; LR = 258.48 at 80 cm, both  $P < 0.0001$ ) (Figure 4).

## Discussion

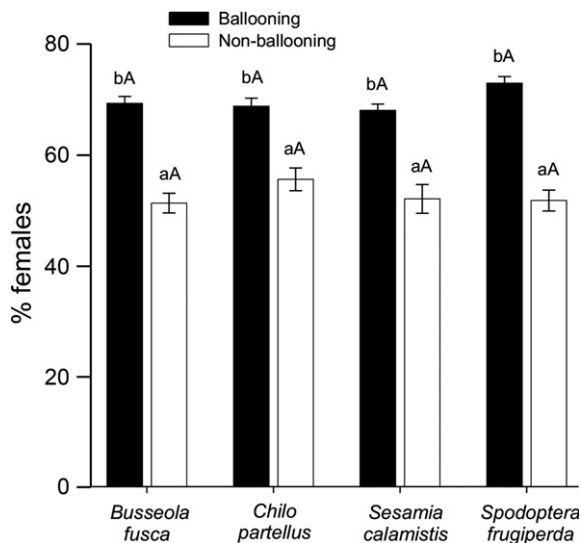
All species studied exhibited ballooning activities. However, this is the first time it has been shown for *S. calamistis*



**Table 1** Mean ( $\pm$  SE) larval and pupal survival rate (%) and development time (days) of ballooning and non-ballooning larvae of fall armyworm (*Spodoptera frugiperda*) and three stemborer species (*Busseola fusca*, *Sesamia calamistis*, *Chilo partellus*) on maize plants

Parameters	Species	Larvae				Pupae			
		Ballooning	Non-ballooning	LR	P	Ballooning	Non-ballooning	LR	P
Survival rate (%)	<i>B. fusca</i>	89.68 $\pm$ 1.96	61.55 $\pm$ 2.14	56.95	<0.0001	91.47 $\pm$ 1.06	69.03 $\pm$ 2.54	56.95	0.004
	<i>S. calamistis</i>	91.08 $\pm$ 1.53	58.98 $\pm$ 2.56	157.92	<0.0001	89.14 $\pm$ 1.29	65.98 $\pm$ 2.30	54.17	<0.0001
	<i>C. partellus</i>	90.50 $\pm$ 1.22	57.84 $\pm$ 2.70	114.62	<0.0001	90.16 $\pm$ 1.26	63.88 $\pm$ 2.68	61.73	<0.0001
	<i>S. frugiperda</i>	85.81 $\pm$ 1.56	63.04 $\pm$ 1.93	82.06	<0.0001	89.19 $\pm$ 2.18	62.09 $\pm$ 2.44	89.15	<0.0001
	LR	6.23	8.13			0.88	7.09		
	P	0.10	0.07			0.82	0.06		
Development time (days)	<i>B. fusca</i>	34.95 $\pm$ 0.18c	35.65 $\pm$ 0.15b	0.13	0.70	9.80 $\pm$ 0.18	10.50 $\pm$ 0.26	1.48	0.47
	<i>S. calamistis</i>	32.10 $\pm$ 0.51bc	34.40 $\pm$ 0.41b	1.59	0.20	10.10 $\pm$ 0.19	11.15 $\pm$ 0.20	1.03	0.30
	<i>C. partellus</i>	29.85 $\pm$ 1.34b	31.80 $\pm$ 0.63b	1.23	0.26	10.35 $\pm$ 0.48	12.15 $\pm$ 0.39	2.88	0.08
	<i>S. frugiperda</i>	20.65 $\pm$ 1.24a	22.65 $\pm$ 1.14a	1.84	0.17	10.40 $\pm$ 0.35	11.55 $\pm$ 0.38	1.20	0.27
	LR	82.88	70.54			0.44	2.54		
	P	<0.0001	0.003			0.93	0.46		

LR = likelihood ratio.

Means within a column followed by different letters are significantly different (Tukey's test:  $P < 0.05$ ).**Figure 3** Mean ( $\pm$  SE) percentage of females from larvae that exhibited ballooning and non-ballooning activity in fall armyworm (*Spodoptera frugiperda*) and three stemborer species. Means within a species capped with different lowercase letters are significantly different (Tukey's test:  $P < 0.05$ ); means within an activity did not differ among species (Tukey's test:  $P > 0.05$ ).

and FAW. Ballooning activity has been recorded in several lepidopteran families, including Cossidae, Geometridae, Lymantriidae, Noctuidae, Psychidae, and Pyralidae (Common & Slater, 1997; Zalucki et al., 2002). Dispersal commonly leads to neonates selecting newly expanding leaves

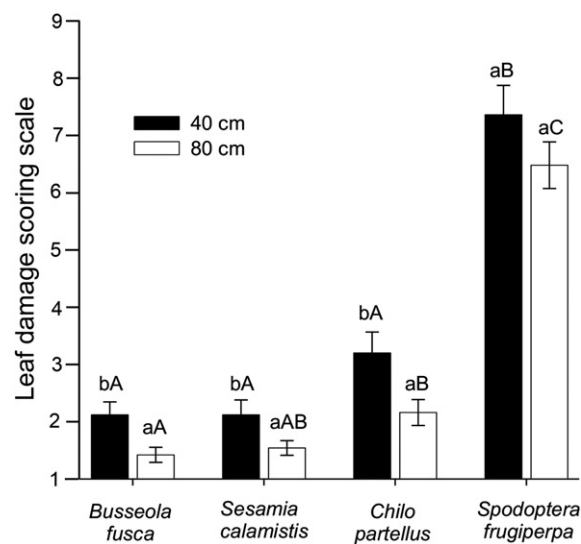
for their first meal (e.g., Joseph & Kelsey, 1994). However, the capacity for ballooning off in neonate larvae depends on the insect species (Zalucki et al., 2002). The percentage of the first instars that disperses by ballooning off is variable, ranging from 1% in *Ostrinia nubilalis* (Hübner) (Razze & Mason, 2012), 15–26% in *Lymantria dispar* (L.) (Diss et al., 1996; Zlotina et al., 1999) to 93% in the common armyworm, *Mythimna convecta* (Walker) (McDonald, 1991). Ballooning activities of 4 and 55% were reported for *B. fusca* and *C. partellus*, respectively (Van Rensburg et al., 1987; Berger, 1989); in the present study it was 30% for both species, not different from the mean values found by the previous studies. In the present study, FAW neonate larvae exhibited greater ballooning activity than stemborers. Several studies suggested that in the cases where larval dispersal is limited, females select for high-quality hosts (van Huis, 1981; Thompson, 1988; Roitberg et al., 1999; Zlotina et al., 1999; Gripenberg et al., 2010; Refsnider & Janzen, 2010; Bellota et al., 2017). Thus, the higher dispersal indicates that FAW is less involved in high-quality host assessment and also more polyphagous than any of the stemborer species. In fact, its host range exceeds 180 species (Sparks, 1979; Andrews, 1980; Pogue, 2002; Casmuz et al., 2010). In this case, dispersal away from hosts carrying more larvae is likely to be mostly adaptive for FAW because it would reduce intraspecific competition and cannibalism (Chapman et al., 1999; Andow et al., 2015). Neonate lepidopteran larvae disperse away from their natal plants for diverse reasons, from avoiding predation and competition to finding suitable hosts

**Table 2** Mean ( $\pm$  SE) number of infested maize plants and number of larvae of fall armyworm (*Spodoptera frugiperda*) and three stem-borer species per plant in a circle with 40-cm radius (five plants in a circle) or 80-cm radius (10 plants in a circle) (see Figure 1)

Species	Infested plants		Larvae per plant	
	40 cm	80 cm	40 cm	80 cm
<i>Busseola fusca</i>	2.60 $\pm$ 0.24a	3.20 $\pm$ 0.58a	1.00 $\pm$ 0.22a	0.38 $\pm$ 0.09a
<i>Sesamia calamistis</i>	2.60 $\pm$ 0.24a	2.80 $\pm$ 0.20a	0.92 $\pm$ 0.20a	0.38 $\pm$ 0.09a
<i>Chilo partellus</i>	3.00 $\pm$ 0.00ab	3.80 $\pm$ 0.37a	0.96 $\pm$ 0.16a	0.50 $\pm$ 0.10a
<i>S. frugiperda</i>	5.00 $\pm$ 0.00b	9.80 $\pm$ 0.20b	2.92 $\pm$ 0.26b	2.36 $\pm$ 0.14b
LR	18.207	78.98	18.20	78.98
P	0.0003	<0.0001	0.0003	<0.0001

LR = likelihood ratio.

Means within a column followed by different letters are significantly different (Tukey's test:  $P < 0.05$ ).



**Figure 4** Mean ( $\pm$  SE) damage score for maize plants in a circle with 40 or 80 cm radius (see Figure 1), damaged by larvae of fall armyworm (*Spodoptera frugiperda*) and three stem-borer species. Means within a species capped with different lowercase letters, and within a radius capped with different uppercase letters, are significantly different (Tukey's test:  $P < 0.05$ ).

(Zalucki et al., 2002; Perovic et al., 2008). In gregarious species the risk of reduced larval fitness as a result of rapidly declining host quality due to overcrowding is high. Thus, population density and host quality may mediate their dispersal from natal hosts (van Huis, 1981; Chapman et al., 1983; Berger, 1992; Price, 1997; Cohen et al., 2000; Dirie et al., 2000; Zalucki et al., 2002; Moore & Hanks, 2004; Lopez et al., 2013; Ramalho et al., 2014; Bernal et al., 2015).

For all species studied, the percentage of females among ballooning larvae that reached the pupal stage was higher than that of non-ballooning larvae. Rhainds et al. (2002)

reported that for larvae of *Metisa plana* Walker, a pest of the oil palm *Elaeis guineensis* Jacquin, the sex ratio of ballooned larvae that attained the pupal stage was consistently female-biased and exceeded 81%. This female-biased sex ratio might be involved in ensuring the perennity of the species (Rossiter, 1987; Lagoy & Barrows, 1989; Rhainds et al., 1998). Sex-specific dispersal behavior by male and female larvae has been reported in other lepidopteran species such as Lymantriidae (Rossiter, 1987; Harrison, 1994) and Psychidae (Cox & Potter, 1988; Rhainds & Gries, 1997; Rhainds et al., 1998). Moreover, for all species under study, ballooning larvae had a higher survival rate than non-ballooning larvae. These results are in contrast to the lower survival rate for ballooning larvae, widely reported in field and semi-field conditions (Carey et al., 1995; Zalucki et al., 2002; Razze & Mason, 2012; Varella et al., 2015). A lower survival rate for ballooning larvae than for non-ballooning larvae can be expected under field conditions, as the ballooning larvae are more prone to abiotic factors such as ambient temperature, dislodgment by rainfall, drowning, and biotic factors, such as landing on an unsuitable plant or being attacked by natural enemies (Zalucki et al., 2002). Meagher & Nagoshi (2004) and Pan-nuti et al. (2015) reported similar higher survival rates in ballooning than in non-ballooning larvae, whereas Reavey & Lawton (1991) emphasized the contribution of larval behavior to their fitness under controlled conditions.

In plant-to-plant movements, in addition to ballooning, neonates may move between plants by lowering themselves on silk threads (Torres-vila et al., 1997), whereas older larvae may migrate by crawling from one plant to another, leading to a decline in stemborers and fall armyworm density on the oviposition plant and an increase in density on adjacent plants. This pattern is similar to that reported for the European corn borer, *O. nubilalis* (Shelton et al., 1986; Ross & Ostlie, 1990) and was already reported

for African stemborers (Van Rensburg et al., 1987; Van Den Berg et al., 1991; Calatayud et al., 2014; Ndjomatchoua et al., 2016). In our study, both the incidence and density of infestation of stemborers decreased significantly with distance from the point of infestation for all stemborers, whereas those of FAW were not affected by distance. In addition, as a pure leaf feeder, FAW larvae produced higher leaf damage and dispersal potential than stemborers. The devastating character in maize fields of FAW has been reported in several studies (Goergen et al., 2016; Srinivasan et al., 2018; Fotso Kuate et al., 2019).

In conclusion, the invasive characteristic of *C. partellus* was not explained by its larval dispersal activity (by either ballooning off or crawling) compared to indigenous stemborers. Other parameters can explain its invasiveness, such as its higher survival rate and higher relative growth rate under interspecific interactions with *B. fusca* and *S. calamistis* (Ntiri et al., 2016). In contrast, FAW neonate larvae had greater potential for ballooning off than those of stemborers, irrespective of species, more females dispersed than males, and their survival rate was higher than that of non-ballooning larvae. In addition, FAW larvae have higher potential to spread between plants than the African maize stemborers, and this might explain, in part, the invasive characteristic of the species. These findings might also help in the production of sampling plans, as larval dispersal directly influences the accuracy of scouting methods (Ross & Ostlie, 1990) and larval survival information increases the precision of economic thresholds (Ostlie & Pedigo, 1987; Ross & Ostlie, 1990).

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