

Cannibalism and intraguild predation involved in the intra- and inter-specific interactions of the invasive fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and lepidopteran maize stemborers

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Abstract

Intra- and interspecific competitions play important role in determining spread and survival/death (cannibalism or intraguild predation) of organisms which share the same resource. However, the trends of relation between cannibalism and intraguild predation, and the costs and benefits of such behaviours are difficult to establish within insect communities and a little is known about how such behaviours are affected by invasive species. The present study was aimed at assessing the interactions between larvae of fall armyworm (*Spodoptera frugiperda*) and maize stemborers (*Busseola fusca*, *Sesamia calamistis* and *Chilo partellus*) in relation to cannibalism and intraguild predation when they are subjected to utilize the same resource. Experiments involving treatments with either single species of *S. frugiperda* or any of the stemborers or pairwise species combinations were conducted under laboratory conditions. The experimental insect larvae were reared on maize leaves and monitored until the last developmental stage where larval survival, mortality, and cannibalism and/or intraguild predation were recorded. Results of the intra-specific interaction indicated that *S. frugiperda* exhibited cannibalism to a larger degree than the stemborers species, especially at the late instars stages. The higher cannibalism trait in *S. frugiperda* turned however to competitive advantage as it led to a higher degree of intraguild predation when they cohabit with other stemborer species. Overall, interaction with *S. frugiperda* is thus detrimental for the stemborer species and may be an important factor to explain the invasive success of the pest. Such knowledge is essential in designing successful integrated pest management strategies.

Key Message

- Understanding the intraguild interactions between pest species with overlapping ecological niches is crucial to predict the impact they will have on species abundance and competitive displacement
- Invasive fall armyworm co-inhabits maize with stemborer species in maize cropping systems.
- The higher cannibalism trait in fall armyworm larvae turned into competitive advantage as it led to a higher degree of intraguild predation when they cohabit with stemborer species
- The higher intraguild predation of fall armyworm on stemborers may impact population dynamics and niche displacement in maize

Introduction

Resource availability varies spatially and temporally either within or across developmental stages and competitive exclusion should result when resources are limited. Such exclusion depends on the biological characteristics of the interacting organisms, where some species may have better competitive abilities. Intra- and interspecific competitions play an important role in determining survival/death and spread of organisms which share the same niche (Cameron et al. 2007; Gurevitch et al. 1992). The interaction between organisms can be expressed as either exploitative (as use of the resource by one species reduces the availability for the other) or interference competition (when one competing species behaviourally restricts the other species from access limited resources supplies). In the most extreme

form of interference competition, the interaction leads to the death of one of the involved organisms and could be defined as a form of either cannibalism or intraguild predation.

Cannibalism, also called intraspecific predation, is known as killing and consumption of a conspecifics (Richardson et al. 2010) and is a widespread behaviour in phytophagous insects, mostly in lepidopteran species (Richardson et al. 2010). It is often favored under high population densities (Sokame et al. 2022) and when resources are limited (Elgar & Crespi 1992) but can occur even when food is not limited (Polis 1981). Intraguild predation (IGP) occurs between different species within the same trophic level (Bentivenha et al. 2016a). Polis & Holt (1992) reported that although combining elements of predation and competition, intraguild predation is distinct from competition because one participant (the predator) accrues immediate energetic gains. It is also distinct from classical predation, because the act reduces potential competition besides the actual energetic gains. Intraguild predation can act as mechanisms of population regulation or as determinants of community structure in phytophagous insect communities (Holt & Polis 1997; Bentivenha et al. 2016a; 2017). Irrespective of whether it is cannibalism or intraguild predation, these behaviours are costly in terms of energy, time, risk of injury and death (Briffa & Elwood 2004; Kelly & Godin 2001) for competing individuals that may have repercussions for an individual's fitness. The balance between cannibalism and intraguild predation depends on involved species. For instance, it was reported that intraguild predation is less frequent than cannibalism for coccinellid species *Ciccinella spetempunctata* L. and *Hippodamia convergens* Guerin-Meneville as compared to the predatory bug *Geocoris bullatus* Say when cannibalism versus intraguild predation was compared among the three species (Takizawa & Snyder 2011). Furthermore, Rasekh & Osawa (2020) reported that two coccinellid species *Harmonia axyridis* and *H. yedoensis* were exposed to either cannibalism or IGP, and *H. axyridis* had longer development time while *H. yedoensis* presented shorter development and lighter adult weight. Therefore, the trends of relation between cannibalism and intraguild predation, and the costs and benefits of such behaviours is difficult to establish. Moreover, there is still little known about how such behaviours are affected by invasive species and how such that could affect crop pests that share the same resources.

In East and Southern Africa, the noctuid stemborers, *Busseola fusca* (Fuller) and *Sesamia calamistis* Hampson, and the crambid *Chilo partellus* (Swinhoe) are key pests of maize and sorghum (Seshu-Reddy 1998; Kfir et al. 2002). Depending on altitude they occur as single species or mixed multi-species communities (van den Berg et al. 1991; Tefera 2004; Ong'amo et al. 2006; Krüger et al. 2008). In addition to these maize pests, the recently introduced Fall Armyworm (FAW), *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae), which was detected in sub-Saharan Africa in 2016 (Goergen et al. 2016) and thereafter spread quickly in Africa (De Groote et al. 2020; Kassie et al. 2020), is currently sharing the same maize plant feeding guild as the pre-existing lepidopteran stemborers (De Groote et al. 2020; Sokame et al. 2020; Goergen et al. 2016). The stemborer larvae feed on young leaves until the third instar from where they bore into the maize stems and then feed from them (Holloway 1998; Polaszek 1998); whereas FAW larvae feed only on leaves throughout their development, especially the central leaves in plant whorl (Morrill & Greene 1973; Van den Berg 1997; Montezano et al. 2018). In addition, in maize fields at tasseling stage, the FAW larvae could be found feeding on the tassels and subsequently on the

ear, silk, cob, and even in stemborer holes in the plant stem (CAB International 2017; Morrill & Greene 1973; Cruz and Turpin 1982) leading them to share the same ecological niche with possible intraguild competition. A previous study reported competition among these four maize pests when they utilize the same resource in a restricted space (Sokame et al. 2020) and the decrease of stemborer density at maize reproductive stage in maize fields following the invasion of FAW in the system (Sokame et al. 2021a) indicates competitive exclusion by FAW since its introduction in Africa. However, the potential of cannibalism and intraguild predation within the community is not well known.

Cannibalism and intraguild predation could contribute to FAW rapid establishment and for interactions in these maize lepidopteran pest communities. In the native range of FAW, cannibalism has been reported (Chapman et al. 1999b; Andow et al. 2015) as well as intraguild predation between FAW and *Helicoverpa zea* (Bentivenha et al. 2016a). Cannibalism has also been reported in *C. partellus*, but only at high larval densities (Bonhof & Overholt 2001). Nevertheless, there is still much to be clarified about the behaviour of the other stemborer species, and interspecific interactions between FAW and these stemborers when they co-occur and the fast and successful establishment of FAW in Africa. A better understanding of the intra- and interspecific interactions will be useful to understand how competitive displacement occurs between those pest species sharing a given ecological niche, and consequently might help to enhance designing successful integrated pest management strategies (Benelli 2015). In this context, the present study aimed at assessing the potential of cannibalism and intraguild predation of the four lepidopteran maize pests species when they are subjected to utilize the same resource and if this can lead to competitive exclusion.

Materials And Methods

Insects

The stemborer and FAW larvae were provided by the Animal Rearing and Containment Unit (ARCU) at *icipe*, Nairobi, Kenya. Larvae were reared on artificial diet in cylindrical plastic jars (16.5 cm high and 9 cm in diameter) with about 200 ml of diet per jar. After inoculation, the plastic jars were tightly sealed using perforated lids with galvanized mesh. They were covered with tissue paper and kept in a rearing room at $26 \pm 1^\circ\text{C}$, $60 \pm 5\%$ RH., and L12 and D12 photoperiod. Twice a year, each colony was rejuvenated with field-collected stemborer or FAW larvae. All insect laboratory rearing was carried out at $25 \pm 2^\circ\text{C}$; 50-70% RH and a photoperiod of 12:12 (L:D) h.

Experimental Set Up

Experiment 1: Cannibalism and intraguild predation involved in fall armyworm and stemborer species larval age-grouped pairing communities

To understand the potential of cannibalism and intraguild predation, an experiment was settled involving treatments with either single species of FAW or any of the stemborers (*B. fusca*: Bf, *S. calamistis*: Sc and *C. partellus*: Cp) or pairwise species combinations between FAW and each of the stemborers. The

experiments were conducted in plastic containers (16 cm × 10 cm × 7cm) lined with a paper towel to absorb excess moisture containing 6 pieces of freshly cut maize leaves (10 cm × 6 cm). The larval instars were structured in three age groups: neonate to second as small size, third to fourth as medium size and fifth and sixth instar as large size. The single-species infestation treatments consisted of 40, 20 and 10 larvae for small, medium, and large size groups, respectively. Those densities were chosen as these densities are usually encountered in the field (Sokame BM. Pers. Obs.). Similar to the method of Bonhof & Overholt (2001) to assess cannibalism between stemborer species, the pairing-species combination involved 20, 10 and 5 larvae per container of each species for FAW+Bf, FAW+Sc and FAW+Cp pairings for each small, medium and large size group, respectively (Table 1). The survival, relative growth rate, mortality (dead larvae found in full corpse), and cannibalism coupled with intra-guild predation (dead larvae found in partial corpse or disappeared corpse) were recorded four (4) days after the settlement (corresponding to the mean time from one instar to another until L5 for FAW) and after five (5) days from L5 to L6, the last instar for pupation.

Table 1

Number of larvae used for each species in the single- and multiple-species combinations tested for each of the three densities of infestation.

Combinations	Larval sizes		
	Small	Medium	Large
FAW	40	20	10
Bf	40	20	10
Sc	40	20	10
Cp	40	20	10
FAW+Bf	20 + 20	10 +10	5 + 5
FAW+Sc	20 + 20	10 +10	5 + 5
FAW+Cp	20 + 20	10 +10	5 + 5
FAW = <i>Spodoptera frugiperda</i> , Bf = <i>Busseola fusca</i> , Sc = <i>Sesamia calamistis</i> , Cp = <i>Chilo partellus</i>			

Experiment 2: Cannibalism and intraguild predation involved in fall armyworm and stemborer species larval life-time pairing communities

To check if cannibalism or intraguild predation continues in all instars and whether individuals that have fed on conspecifics gain some advantages, a second experiment was conducted. It involved single species infestation of either fall armyworm (FAW) or any of the stemborers (*B. fusca*: Bf, *S. calamistis*: Sc and *C. partellus*: Cp) larvae and pairwise multi-species infestation of FAW and stemborers was settled with larval neonate instar. The single-species infestation treatments consisted of 20 neonates while the pairing-species combination involved 10 neonates of each species per container. The same parameters

as described in experiment 1 above were evaluated from neonate to the last instar larvae for pupation with four (4) days interval.

For both the experiments after the infestation, plastic containers were closed with perforated plastic lids until the experiment terminated. The insects in the container were kept in a rearing room at a temperature of $25 \pm 0.05^\circ\text{C}$, RH of $58.5 \pm 0.4\%$, and a photoperiod of L12:D12. Each treatment was replicated twenty times. Like the method of Bonhof & Overholt (2001), after 4 days, containers were opened to record the number of surviving larvae (Ns) and the number of dead larvae (Nd) of each species. The cannibalism (C) in single-species communities and both cannibalism and intraguild predation (C&IGP) in multi-species communities were calculated as follow:

$$Cor(C\&IGP) = N - (Ns + Nd)$$

Where N denoted the initial number of larvae inoculated in each container.

The relative growth rate (RGR) for each species was calculated using the following equation (Ojeda-Avila et al., 2003):

$$RGR = \frac{\text{Masspersurvivinglarva} - \text{Initialmassperlarva}}{\text{Numberofdaysafterpairingspecies}}$$

Data Analyses

The number of surviving larvae, the number of dead larvae and the number of larvae that have been consumed (cannibalism and intraguild predation) from either experiment 1 or experiment 2, were analysed using a generalized linear model (GLM) with negative binomial procedure. Significant differences were separated using Tukey's multiple comparison test performed using the R package "lsmeans" (Lenth 2016). The relative growth rate (RGR) of the larvae from the two experiments were analysed using Kruskal-Wallis nonparametric procedure with `dunn.test` R package after being tested for normality and homogeneity of variance using Shapiro-Wilk and Bartlett tests, respectively. All analyses were performed with R software version 3.5.1 (R Core Team 2018).

Results

Survival, mortality, and cannibalism of fall armyworm and stemborers in single-species combination

At small larval size, FAW had the lowest survival rate while *B. fusca* had the highest (LR = 26.38, df = 3; $P \leq 0.0001$). At medium larval size group, no significant difference was recorded between the four species (LR = 3.01, df = 3; $P = 0.39$) while at large larval size group, the survival rates of the three stemborer species were significantly higher than those of FAW (LR = 31.66, df = 3; $P \leq 0.0001$) (Fig. 1A). Between larval size groups for a given species (Fig. 1A), the survival rate of FAW was significantly lower at large

size group as compared to the smaller size groups ($\chi^2 = 22.30$; $df = 2$; $P \leq 0.0001$) in opposition to *C. partellus* where higher survival rate was recorded at larger size group ($\chi^2 = 16.45$; $df = 2$; $P \leq 0.0001$). For *B. fusca*, survival rate was significantly low at medium size group as compared to small and large size groups ($\chi^2 = 6.72$; $df = 2$; $P = 0.03$) while no significant difference was recorded between *S. calamistis* larval sizes ($\chi^2 = 5.30$; $df = 2$; $P = 0.07$).

In terms of mortality (Fig. 1B), there was no significant difference between the four species at small larval size group ($\chi^2 = 7.57$; $df = 3$; $P = 0.06$). However, at medium size group, *B. fusca* presented a significantly higher mortality rate than FAW ($\chi^2 = 22.23$; $df = 3$; $P \leq 0.0001$), while at large size group, *C. partellus* mortality was significantly lower as compared to FAW and *B. fusca* ($\chi^2 = 25.37$; $df = 3$; $P \leq 0.0001$). Between larval size groups for a given species, large size of FAW presented a significant higher mortality as compared to small and medium size groups ($\chi^2 = 16.62$; $df = 2$; $P \leq 0.0001$). The mortality rates of *B. fusca* were significantly higher at medium and large size groups than at small size group ($\chi^2 = 5.17$; $df = 2$; $P = 0.04$) while they were significantly higher at small and medium size groups than large size group for *C. partellus* ($\chi^2 = 12.25$; $df = 2$; $P \leq 0.0001$). No significant difference was revealed between the different size groups of *S. calamistis* ($\chi^2 = 1.45$; $df = 2$; $P = 0.48$).

The cannibalism rate (Fig. 1C) was significantly more pronounced in FAW than in stemborer species at all larval size groups, small ($\chi^2 = 58.76$; $df = 3$; $P \leq 0.0001$), medium ($\chi^2 = 46.63$; $df = 3$; $P \leq 0.0001$) and large size ($\chi^2 = 105.61$; $df = 3$; $P \leq 0.0001$). On the other hand, while the higher cannibalism rate of FAW was recorded at large size group ($\chi^2 = 8.01$; $df = 2$; $P = 0.02$), it was the lower rate that was recorded for *B. fusca* ($\chi^2 = 11.16$; $df = 2$; $P \leq 0.0001$), *C. partellus* ($\chi^2 = 19.66$; $df = 2$; $P \leq 0.0001$) and *S. calamistis* ($\chi^2 = 18.96$; $df = 2$; $P \leq 0.0001$) at that larval size group as compared to small and medium age groups.

Survival, mortality, and cannibalism coupled with intraguild predation in pairing-species combination between fall armyworm and stemborers

For all combinations, FAW survival rate was significantly higher than that of its corresponding competing species at all larval size groups: FAW+Bf (Fig. 2A, Table 2), FAW+Sc (Fig. 2B, Table 2) and FAW+Cp (Fig. 2C, Table 2). There was no significant difference for mortality within species in all combinations at small larval size group: FAW+Bf (Fig. 2D, Table 2), FAW+Sc (Fig. 2E, Table 2) and FAW+Cp (Fig. 2E, Table 2). However, the mortality of FAW was significantly higher in the pairing with *B. fusca* at medium and large larval size groups (Fig. 2D, Table 2), with *S. calamistis* at medium and large larval size groups (Fig. 2E, Table 2) and with *C. partellus* at medium and large larval size groups (Fig. 2F, Table 2). The cannibalism coupled with intraguild predation of stemborer species were significantly higher than that of FAW in all combinations at all larval size groups: FAW+Bf (Fig. 2G, Table 2), FAW+Sc (Fig. 2H, Table 2) and FAW+Cp (Fig. 2I, Table 2).

Table 2

Results of GLM analysis comparing larval survival, mortality and cannibalism/intraguild predation between fall armyworm vs stemborer species in multi-species combinations at different development stages

Combinations	Larvae development stages								
	Small			Medium			Large		
	LR	df	P	LR	df	P	LR	df	P
Survival									
FAW+Bf	45.41	1	≤ 0.0001	82.85	1	≤ 0.0001	28.03	1	≤ 0.0001
FAW+Sc	47.72	1	≤ 0.0001	30.75	1	≤ 0.0001	6.95	1	0.008
FAW+Cp	54.45	1	≤ 0.0001	28.87	1	≤ 0.0001	25.30	1	≤ 0.0001
Mortality									
FAW+Bf	0.22	1	0.63	4.6	1	0.04	6.05	1	0.01
FAW+Sc	0.86	1	0.35	6.73	1	0.009	10.35	1	0.001
FAW+Cp	0.02	1	0.88	11.82	1	0.0005	12.20	1	0.0004
Cannibalism/intraguild predation									
FAW+Bf	82.47	1	≤ 0.0001	49.11	1	≤ 0.0001	26.95	1	≤ 0.0001
FAW+Sc	62.41	1	≤ 0.0001	28.73	1	≤ 0.0001	10.35	1	0.001
FAW+Cp	49.14	1	≤ 0.0001	22.88	1	≤ 0.0001	28.90	1	≤ 0.0001

Comparison of survival, mortality, and cannibalism and/or intraguild predation in single- versus pairing-species combinations

For this comparison purpose, the survival, mortality, and cannibalism and/or intraguild predation rates were calculated for the overall larvae regardless of the species present in each test for pairing-species combinations. All stemborer single-species combinations exhibited a significant higher survival rate than their respective pairing-species combinations with FAW at all larval size groups (Fig. 3, small: LR = 202.62; df = 6; $P \leq 0.0001$, medium: LR = 146.56; df = 6; $P \leq 0.0001$ and large: LR = 127.78; df = 6; $P \leq 0.0001$).

At small size group, stemborer single-species communities presented a higher mortality than their respective pairing-species combination with FAW (LR = 24.86; df = 6; $P = 0.0003$). At medium size group, while FAW had lower mortality, *B. fusca* single-species had significantly higher mortality as compared to its pairing-species combination counterpart mortality (LR = 28.69; df = 6; $P \leq 0.0001$). At large size group, *S. calamistis* and *C. partellus* single-species combinations exhibited significantly lower mortalities as

compared to the mortalities of their pairing-species combination counterparts (LR = 35.14; df = 6; $P \leq 0.0001$).

The cannibalism coupled with intraguild predation in pairing-species combination was significantly higher as compared to cannibalism in single-species combinations at all larval size groups (Fig. 3, small: LR = 349.81; df = 6; $P \leq 0.0001$, medium: LR = 356.83; df = 6; $P \leq 0.0001$ and large: LR = 246.41; df = 6; $P \leq 0.0001$).

Life-time survival, relative growth rate, mortality, and cannibalism of fall armyworm and stemborers across larval instars in single-species combination

Across larval instars, the three stemborers species presented similar survival evolution while significantly higher than those of FAW species from third to sixth instar (Fig. 4A, $\chi^2 = 308.17$; df = 5; $P = 0.0001$). The FAW presented the greater relative growth rate as compared to those of stemborers at third and fourth instars with an optimum of 15mg/day (Fig. 4B).

The Fig. 4C present the evolution of mortality rate of the different species across larval development instars. At L1 instar, *S. calamistis* presented a high mortality rate as compared to other species ($\chi^2 = 26.93$; df = 5; $P = 0.0001$). However, at L5 and L6 instars, the mortality rate of FAW became significantly lower while those of stemborer species were still high L5 ($\chi^2 = 37.94$; df = 3; $P = 0.02$), L6 ($\chi^2 = 98.23$; df = 3; $P = 0.03$). The cannibalism rate (Fig. 4D) was significantly higher in FAW than in stemborer species from third to last instar, L3 ($\chi^2 = 56.7$; df = 3; $P = 0.01$), L4 ($\chi^2 = 34.92$; df = 3; $P = 0.002$) L5 ($\chi^2 = 95.78$; df = 3; $P = 0.03$) and L6 ($\chi^2 = 123.54$; df = 3; $P \leq 0.0001$).

Life-time survival, relative growth rate, mortality and cannibalism coupled with intraguild predation across larval development instars in pairing-species combinations

In pairing-species combination between fall armyworm and stemborers, none of stemborer species survived at the last instar to pupate (Fig. 5A1-A3). The survival rate of either FAW or stemborers significantly decreased along larval development instars ($\chi^2 = 42.52$; df = 5; $P = 0.001$) and the survival of FAW was significantly higher than those of stemborers in each combination ($\chi^2 = 57.13$; df = 3; $P = 0.004$). *B. fusca* and *S. calamistis* reached 0% at L4 instar and *C. partellus* at L5 instar while about 10% of FAW survived at last instar to pupate. The growth rate of stemborer species did not reach the optimum before they disappeared in the combinations (Fig. 5B1-B3). The optimum of FAW growth rate ranged from 40 to 50mg/day across the different combinations and it has mostly decreased after stemborer species were no longer present in the combinations (Fig. 5B1-B3). In each pairing-species combination, the mortality rate of stemborers was significantly ($\chi^2 = 32.34$; df = 3; $P = 0.001$) higher than those of FAW along larval development instars before the optimum and thereafter, the mortality rate of FAW come over those of stemborer species (Fig. 5C1-C3). on the other hand, the cannibalism coupled with intra-guild predation of stemborers in each combination was significantly higher than those of FAW along larval development

instars ($\chi^2 = 54.21$; $df = 3$; $P \leq 0.0001$). However, when they finished in the system, the cannibalism of FAW presented exponential trend (Fig. 5D1-D3).

Discussion

The polyphagous feeding habitat (Montezano et al. 2018), voracity (Wan et al. 2021), the high potential economic loss in crops (Wang et al. 2020) and the recent invasion in Africa (Goergen et al. 2016) of fall armyworm have created significant interest in its potential interactions with maize stemborer species. Our results indicated that FAW exhibited cannibalism to a larger degree than stemborers species, especially in the late instars. The large degree of cannibalism in FAW may contribute to their relatively lower survival in single species cohorts. The cannibalistic behaviour of FAW has already been well documented, both in laboratory and under field conditions (Chapman et al. 2000; Goussain et al. 2002). In the present study when the larvae were followed from neonate to last development stage, the cannibalism was observed mostly from 3rd instar with a maximum level at 5th and 6th instars indicating the positive correlation between the cannibalism phenomenon and the aggressivity of the insect when becoming large (Bentivenha et al. 2016b). Chilcutt (2006) and Horner et al. (2009) have reported that in Noctuid insects, cannibalism is dependent on the insect development instar with a tendency to more frequently occur in larger than smaller larvae. In addition to the high cannibalism rate recorded in FAW as compared to other species, there also seems to be some intrinsic mortality in FAW, especially in the largest instar. Several studies have shown that larvae which end up practicing cannibalism may have high mortality by suffering injuries and death acquiring pathogens and parasites, having subsequent reduction in fitness which might differ between native and invasive insect species (Bentivenha et al. 2016; Chapman et al. 1999a,b; Rudolf & Antonovics 2007).

Invasive species are generally less frequently infected in introduced environment as compared to native conspecific populations (Torchin & Mitchell 2004). Successful introduced species often invade without their native parasites and accumulate relatively few new ones in the invaded areas. This suggest that costs- and benefits of cannibalism differ in native and invaded area depending on whether they experience less or more parasites and pathogens in these areas. In the other hand, it has been reported that FAW cannibalism rates were around 18%, when confined to maize seedlings and can increase up to 34% in case of limited food and even reach 100% when the larvae are confined in Petri dishes (Bentivenha et al. 2016; Raffa 1987). The suitability of food in terms of quality on which the insect larvae were reared is also a source of cannibalism increase. Therefore, it would be interesting to study how cost-benefits of cannibalism/intraguild predation could differ depending on host plant species.

In interspecific interactions, the higher cannibalism in FAW turns however to competitive advantage when they cohabit with stemborer species. Cannibalism/intraguild predation is higher on the stemborers, and survival is always higher for FAW. The FAW larvae might possess defence mechanism in detriment of other species. Bentivenha et al. (2017a) studied intraspecific interactions of FAW larvae and reported that they exhibited either high attack (head touching) or defense (recoiling) as the prevalent movement and that the frequency of these movements increased with larval development because of their increased

interaction with other larvae when they become bigger and more mobile. These results suggest that there is a great chance that FAW can prevail over these other species and colonize the niche (Bentivenha et al. 2016b; Bentivenha et al. 2017b), when these species occur in maize fields (on plants). Intraguild studies of FAW and *H. zea* showed further advantage of FAW in interaction against *H. zea* in morphological characteristic such as integument or mandible architecture (Bentivenha et al. 2016a), which also could explain the success of FAW during intraguild competition. The intrinsic cannibal character of FAW might prepare the species to a high cost of fight within themselves (actions of defence and attack) in the situation of conspecific cannibalism which explain the lower relative growth rate. In interspecific competition, the actions of the co-existing stemborers which probably go into defense behaviour rather attack, inflict lower fight cost to FAW by the lack of attack actions. Therefore, FAW take the advantage by reducing the cannibalism on their conspecific and concentrate on intraguild predation on their heterospecific species where it is more easy to feed on stemborer larvae with less energy invested, explaining the great relative growth rate gained when reared together with stemborer species than when reared lonely as single species. Arnott & Elwood (2009) have studied those variations of the weight by assessing fighting ability in animal contests and reported that the gain of the weight of the superior from the competition is positively correlated to the contest duration and the cost or intensity of the fight. The competition between FAW and stemborers may be short duration with low-cost than between FAW conspecific species.

The optimum of FAW growth rate ranged from 40 to 50mg/day in cannibalism coupled with intraguild predation with stemborer species while when reared lonely as single species, the growth rate reached an optimal of 30mg/day only. These results are in contradiction with other studies in the literature (e.g. Bentivenha et al. 2016a,b; Ongaratto et al. 2021), where the weight of FAW reared alone as single species and not in competition with other species was significantly greater than the weight of those that surviving the competition with other heterospecific species. However, in the present study, the competition was asymmetric that favour FAW because, while FAW exhibited simultaneously defense and attack behaviour, stemborer species might exhibit only defense behaviour.

The higher intraguild predation of FAW on stemborer species when they are forced to co-habitat indicates a potential competitive advantage of FAW and could be a factor explaining its success as an invasive pest species. However, this analysis needs to be done at large scale as a complex system because other parameters such as agricultural landscape (Bentivenha et al. 2016a), the food quality of the host plant and larval behaviour (Dial & Adler 1990) may influence also intraguild interactions. Intraguild predation may be an important factor during invasion to decrease competition from other species, but in the present study, it does not seem to lead to a higher absolute survival rate of FAW, only a relatively better survival in comparison to the other species. This can be due to that FAW reverses cannibalism behaviour in detriment of intraguild predation when the heterospecific species disappears/is eradicated from the system when FAW are in the later instars. Linked to this great competitive advantage of FAW over stemborer species highlighted in this study, FAW tend to dominate stemborers in maize cropping systems where they co-habituate with a possible displacement of stemborers by FAW elsewhere; for example, to other cereal (Hailu et al. 2021; Sokame et al. 2021a). Historical data of stemborer infestations compared

to the recent evaluations in maize and sorghum cropping systems in Uganda showed a significant decline of the infestations in maize fields in detriment to sorghum fields from 2016, suggesting an early arrival of fall armyworm in Uganda, indicating a possible displacement of stemborer from maize onto sorghum (Hailu et al. 2021). Furthermore, through intense intraguild predation, fall armyworm can reduce the population density and impact of stemborer guild members in maize fields, as the larvae preferred to feed on stemborers rather than their conspecific in interspecific communities. However, if the guild of fall armyworm is to contribute to the suppression of stemborer species population in the context of integrated pest management (IPM) programme, then it necessary that its impact on those stemborers is reliably assessed at an appropriate ecological scale so that the impact on the population dynamics of the pest can be quantified and integrated into decision-making processes for management.

Overall, interaction among FAW and stemborer species in the case of this study affect their survival and FAW gain competitive advantage in intraguild interaction with stemborer species in detriment of cannibalism with their conspecifics. This gives an advantage of FAW over maize stemborers resulting of an overall reduction in stemborer density generally observed in maize fields in Kenya at the beginning of the season (Sokame et al. 2021a), a displacement of some of them to other cereals in Uganda (Hailu et al. 2021). However, the specificity of FAW to feed on leaves and stemborers to plant stems in late instars might result in the co-existence fall armyworm with stemborer species in maize agroecological zones (Sokame et al. 2020, 2021b). Therefore, the invasion of FAW in Africa constitutes an additional pest to crops in agroecosystems that need to be considered within the context of integrated pest management strategies.

Declarations

Authors contributions

BMS, P-AC, PA, and GKK designed the studies. BMS, and BM collected the data. BMS analysed the data and wrote the manuscript. All authors reviewed and approved the manuscript before submission.

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Compliance with ethical standards

Conflicts of interest: The authors declare that they have no conflicts of interest.

Ethical approval: This research complied with all local and national standards for ethical conduct in research. This research did not involve vertebrates or humans, and thus, no IRB approvals were needed.

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Figures

Figure 1

Survival (A), mortality (B) and cannibalism rates (C) of *Spodoptera frugiperda* (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc), and *Chilo partellus* (Cp) in single-species combinations at different larval stages: small size (neonate to second instar), medium size (third to fourth instar) and large size (fifth to sixth instar). Means (\pm SE) with different letters are significantly different, determined using Tukey's multiple comparisons tests performed with lsmeans R package, following generalized linear model (GLM) with negative binomial procedure (comparison between species, lower case letters) and Kruskal-Wallis nonparametric procedure with dunn.test R package (comparison between larval sizes of a given species, upper case letter).

Figure 2

Survival (A-C), mortality (D-F) and cannibalism coupled with intraguild predation rates (G-I) of *Spodoptera frugiperda* (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc), and *Chilo partellus* (Cp) in pairing-species combinations at different larval stages: small size (neonate to second instar), medium size (third to fourth instar) and large size (fifth to sixth instar). Means (\pm SE) with different letters are significantly different, determined using Tukey's multiple comparisons tests performed with lsmeans R package, following generalized linear model (GLM) with negative binomial procedure.

Figure 3

Survival (A), mortality (B) and cannibalism coupled with intraguild predation rates (C) of all larvae regardless of the species between single-species and pairing-species combinations at different larval stages: small size (neonate to second instar), medium size (third to fourth instar) and large size (fifth to sixth instar). Statistical comparisons were only considered between single- and corresponding multi-species pairings. Means (\pm SE) were compared using Tukey's comparisons tests performed using lsmeans R package, following generalized linear model (GLM) with negative binomial procedure. *Spodoptera frugiperda* (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc), and *Chilo partellus* (Cp).

Figure 4

Evolution of survival (A), relative growth rate (B), mortality (C) and cannibalism rates (D) of *Spodoptera frugiperda* (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc), and *Chilo partellus* (Cp) in single-species combinations from neonate to last instar larvae.

Figure 5

Evolution of survival (A1-A3), relative growth rate (B1-B3), mortality (C1-C3) and cannibalism coupled with intraguild predation rates (D1-D3) of *Spodoptera frugiperda* (FAW), *Busseola fusca* (Bf), *Sesamia calamistis* (Sc), and *Chilo partellus* (Cp) in pairing-species combinations from neonate to last instar larvae.